No-take marine reserve performance under varying environmental and anthropogenic influences

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Abstract

Conserving coral reef fish assemblages is important, for ensuring food security for coastal human populations, and for maintaining coral reef ecosystem processes. Sound management of coral reef fish assemblages is a priority, but for management strategies to be truly effective, there is a need to understand what maintains fish assemblages under multiple environmental conditions. No-take marine reserves (NTMRs) are a relatively simple and cost-effective management strategy for conserving marine biodiversity and enhancing food security, particularly in developing island nations with multi-species fisheries. But whether NTMRs can continue to provide social, economic and conservation benefits in the face of increasing environmental threats to coral reefs remains unresolved, and scientific opinion remains divided. Thus, this thesis investigated the relative roles of NTMRs and environmental factors in determining the structure of coral reef fish assemblages. These environmental factors included natural spatial variability in environmental conditions that occurs across continental shelfs, and among and within islands, as well as large-scale environmental disturbance events (cyclones/typhoons, thermal coral bleaching). Specifically, this thesis had four research questions that were addressed in each of four data chapters (Chapters 2-5): 1. How do severe disturbances affect coral reef fish assemblages that develop along prevailing environmental gradients, irrespective of NTMRs? 2. Do NTMRs remain effective as fisheries management tools despite being located in different environments and despite severe environmental disturbances? 3. What are the relative roles of habitat, island geomorphology and NTMRs in driving abundance and species richness of coral reef fishes? 4. Do differences in environmental conditions among coral reef locations result in dietary plasticity of important subsistence fishery species?

Chapter 2 assessed how severe environmental disturbance events affect the structure of coral reef fish assemblages formed along a prevailing environmental gradient, by comparing fish assemblages from the inner-, mid-, and outer-shelf of Australia's Great Barrier Reef (GBR), before and after disturbance impacts, irrespective of NTMR effects. Specifically, changes in benthic cover, and the biomass, taxonomic and trait composition of herbivorous reef fish assemblages were compared at each shelf position, five years before (2008/9), and six months after (2016) two severe cyclones and a thermal bleaching event. Results showed that there was a severe loss of hard coral cover across the shelf following disturbance events (inner-shelf: ~25% to 2%, mid-shelf: ~45% to 5%, outer-shelf: ~60% to 10%), and a substantial loss of fish species trait richness at each shelf position (inner-shelf: 0.23 to 0.06, mid-shelf: 0.3 to 0.16, outer-shelf: 0.24 to 0.07). Taxonomic assemblages of fishes remained distinct at each shelf position before and after disturbance events, with assemblages becoming more distinct both among, and within shelf positions following disturbances. This was attributed to assemblages at each shelf position going from being characterised by multiple species before the disturbances, to being dominated by few or single species following disturbances. These dominant species increased in biomass significantly on mid- and outer-shelf reefs, but not on inner-shelf reefs. Trait-based analyses of the fish assemblages showed increases in trait specialisation and originality on inner-shelf reefs only, indicating a loss of redundancy within the inner-shelf herbivorous reef fish assemblage. Macroalgal cover increased on inner-shelf reefs from 50 to 70% following disturbances. Given the differential response of inner-shelf reef benthic and fish assemblages to environmental disturbances, inner-shelf reefs may have a different recovery rate and trajectory than mid- and outer-shelf reefs considering their exposure to lower water quality.

Chapter 3 compared coral reef fish assemblages among multiple NTMRs and adjacent fished areas in a complex reefscape in the Philippines, to understand whether NTMRs can remain effective as fisheries management tools (i.e. maintain higher fish biomass than fished areas) irrespective of typhoon damage and variability in island types. Coral reef benthic and fish assemblages were compared among 17 habitat matched NTMR-fished control sites across three mainland and four offshore islands that differed in geomorphology and exposure to recent typhoons. NTMRs did not influence the assemblage structure of the benthos, or total hard coral cover relative to fished areas. However, NTMRs had a lower cover of macroalgae than fished areas, particularly on mainland islands. Typhoons had severe negative effects on live hard coral cover, which resulted in a modified fish assemblage structure, and a lower total biomass of fish, irrespective of island type or NTMR protection. There were inherent differences in the assemblage structure of both benthos and fish between mainland and offshore islands, likely attributed to the prevailing environmental conditions of lower water quality on mainland island reefs, compared to the relatively clear water and high wave exposure environments on offshore island reefs. There was also a lower biomass of fish on mainland compared to offshore islands. However, NTMRs consistently had a higher total biomass of fish compared to fished areas, irrespective of island type or typhoon damage. This suggests that NTMRs can provide benefits to fish biomass and thus adjacent fisheries, even among different environmental conditions, and when reefs and habitat for fishes are affected by typhoons.

To understand whether bottom-up (trophic and habitat resources) or top-down (predation pressure) processes have a greater influence on determining fish assemblages, **Chapter 4**

assessed the relative influence of habitat, island spatial characteristics, and fishing on target and non-target fish groups in a multi-species fishery in the Philippines. Boosted regression trees were used to model the response of the abundance and species richness of four coral reef fish groups targeted by fishing, and the abundance of two groups not targeted by fishing, to 20 predictor variables that included no-take marine reserve (NTMR) presence-absence, and NTMR age and size. Fish groups most strongly responded to bottom-up variables of habitat, followed by spatial characteristics, with top-down control of NTMRs being influential only on fishes targeted by fishing. Encouragingly, NTMRs did not have to be large in size to increase fish density and species richness relative to fished areas. This is an important finding for small-scale, community managed initiatives like those in developing nations. This study has important implications for the development of integrated management strategies that prioritize maintaining habitat (defined here as a bottom-up process) for fishery species.

Given the clear importance of the environment in determining fish assemblages, as seen in Chapters 2-4, **Chapter 5** employed stable isotope techniques and manipulative experiments to investigate whether environmental differences among and within islands resulted in dietary plasticity of important subsistence fishery species. Firstly, environmental indicators of sedimentation rates, turf algal productivity, and $\delta^{15}N$ isotopic signatures in the seaweed *Sargassum* were compared among six sites across three islands in the Philippines to establish whether terrestrially derived sediment (and thus nutrient) inputs onto coral reefs varied among sites. Sediment loads, measured using sediment traps, did vary among sites and appeared to affect nutrient availability, with reefs furthest from terrestrial influence having low sediment loads and $\delta^{15}N$ depleted *Sargassum*, while the reef closest to a large tourist resort had the highest sediment loads and most $\delta^{15}N$

enriched *Sargassum*. Turf algal productivity was measured with manipulative cage experiments at each of the six sites. There was generally lower turf algal productivity with increased sedimentation rates, and generally higher productivity under low sedimentation rates, indicating excessive sediment may inhibit turf algal growth. Given environmental differences among the six sites, the diets of three valuable subsistence fishery species common to each site were then investigated using Bayesian stable isotope mixing models to link primary food sources to individual fish. The muscle tissue of three fish species known to have different diets (an algal grazer, an algal browser, and a planktivore) were sampled from each site for analysis of $\delta^{15}N$ and $\delta^{13}C$ isotope signatures. Potential dietary sources of these fish, of turf algae (from experimental tiles), turf algal detritus, the macroalgae *Sargassum*, and zooplankton, were sampled from each site for stable isotope ($\delta^{15}N$ and $\delta^{13}C$) analysis. The proportion of each dietary source in the muscle tissue of each individual fish from each site was then estimated using the mixing model siar (stable isotope analysis in R). Despite the apparent differences in terrestrial inputs of sediment, and differences in turf algal productivity among sites, there was inconclusive evidence that fish species changed primary dietary sources among sites. However, fish species were feeding on some unexpected sources. The algal grazing fish species (*Siganus virgatus*) was consuming moderate proportions of plankton, while the planktivorous species (*Naso minor*) was consuming benthic fleshy macrophytes. With human influences modifying coral reef habitats and fish assemblages throughout the tropics, understanding how ecologically and economically important reef fish species persist remains a question of significance.

Overall, this research increases our understanding of the processes that maintain coral reef fish assemblages under varying environmental conditions and NTMR protection.

While NTMRs remain an important and successful tool in subsidising fisheries and maintaining species assemblages for those fishes targeted by fishing, it is clear that environmental conditions are the stronger driver shaping fish assemblages and coral reef ecosystems. This thesis thus has important implications for informing and improving management strategies in a time of climatic uncertainty. While enhancing capabilities of coral reef management is important globally, it is particularly pertinent for developing island nations that rely heavily on marine resources for food security, and therefore rely on the success of small-scale management initiatives, such as NTMRs. Prioritising management goals to incorporate sound land-use practices that reduce sediment and nutrient inputs onto coastal reefs, and that place NTMRs in areas less prone to land-based impacts and typhoon paths, will help ensure habitat for fishes, and thus, fisheries for the future.

Table of Contents

List of Tables

List of Figures

Figure 5.5. The proportional contribution of food sources to the diets of each consumer species among sites 1. Bononon, 2. Apo, 3. Tubod, 4. Paliton, 5. Cangbagsa. Sites 3-4 are combined for *Naso minor* as fishing gear sampled both together. Percentage proportions with 25% (dark grey), 75% (medium grey) and 95% (light grey) credibility interval (CI) levels. Lower limits of CIs give confidence in proportional contribution. e.g. Lower 95% CI >0.0 indicates the source is contributing to consumer diet (within the bounds of CIs). Lower 95% CIs touching zero indicates uncertainty on the proportional contribution of a source. Lower 25% touching zero, the source is unlikely contributing to the diet of the consumer. Refer to Table S5.4 for siar model outputs for each species. …...…….96

Chapter 1: General Introduction

The conservation of biodiversity in nature is integral to the maintenance of ecological processes, and ecosystem goods and services enjoyed by humanity (Cardinale et al. 2012). Human exploitation of the natural world has seen the degradation of habitats and the decline in diversity of species across ecosystems, thus compromising ecosystem processes (Balmford et al. 2002, Cardinale et al. 2012). A key strategy for conserving ecosystem processes is the designation of protected areas or reserves, where human degradation of habitat or extraction of plant, animal or mineral resources is prohibited (see Lubchenco et al. 2003, Naughton-Treves et al. 2005). Protected areas have proven successful in maintaining habitat and biodiversity on land- (Naughton-Treves et al. 2005) and in seascapes (Allison et al. 1998, Lubchenco et al. 2003) on a local scale, thus supporting human use and enjoyment through resource replenishment, and the intrinsic value that comes with conserving wild nature (Balmford et al. 2002). However, as threats to ecosystems increasingly extend beyond local scale management efforts like reserves (Heller and Zavaleta 2009), a renewed understanding of the role of reserves in maintaining species assemblages compared to local and global drivers is necessary for improving conservation strategies across ecosystems, including tropical coral reefs.

Tropical coral reefs are among the most biodiverse and valued ecosystems on the planet (Reaka-Kudla 1997, Knowlton et al. 2010). Such biodiversity is shaped by a suite of environmental processes and biophysical drivers that operate over a range of spatial and temporal scales (Huston 1985, Ricklefs 1987, Mora et al. 2003), such as temperature, water quality, wave action, disturbance regimes, nutrient availability, and competitive and predatory interactions (Huston 1985, Shears and Babcock 2002, Mora et al. 2003, Fabricius et al. 2005). This biodiversity contributes to the goods and services coral reefs

provide, subsequently being used and relied upon by millions of people as a source of food and income (Newton et al. 2007, Hoegh-Guldberg et al. 2010, Kronen et al. 2010, Stoeckl et al. 2011, Teh et al. 2013). Coral reef fish assemblages are particularly vital in supporting ecosystem services (Holmlund et al. 1999), and human populations through fishing (Newton et al. 2007, Hoegh-Guldberg et al. 2010, Teh et al. 2013). Thus, conserving coral reef fish assemblages is of paramount importance throughout their distribution.

No-take marine reserves (NTMRs) are an important management strategy for conserving biodiversity of coral reef fishes and for helping to sustain coral reef fisheries (Lubchenco et al. 2003). With increasing years from establishment, NTMRs can increase fish biomass and diversity of target species inside reserves (Polunin and Roberts 1993, Denny et al. 2004, Russ et al. 2004, Samoilys et al. 2007, Babcock et al. 2010, Russ and Alcala 2011, Rasher et al. 2013) then export this benefit across their borders to adjacent sites in the form of adult fish (Roberts et al. 2001, Russ et al. 2003, Abesamis and Russ 2005, Russ and Alcala 2011, McClanahan and Mangi 2000, da Silva et al. 2015), and larvae (Almany et al. 2007, Christie et al. 2010, Harrison et al. 2012). These benefits are enhanced further via NTMR networks, connecting reserves and fished areas across ecologically meaningful spatial scales for fishes (Gaines et al. 2010, Weeks et al. 2014, Green et al. 2014; 2015). Through these mechanisms, NTMRs can potentially replenish fisheries and support the livelihoods of communities (Russ et al. 2004, Alcala and Russ 2006, Tobey and Torell 2006, Fletcher et al. 2011, Almany et al. 2013). While NTMRs can prevent direct human destructive and extractive practices when compliance is high (see Samoilys et al. 2007, Campbell et al. 2012, Bergseth et al. 2015), they cannot prevent a multitude of threats that can pass across their boundaries (Lubchenco et al. 2003, Roberts et al. 2017, Jones et al. 2004, Samoilys et al. 2018). Thus, the ability of NTMRs

to continue to provide benefits for nature and humanity, in light of increasing threats of environmental and anthropogenic origin, is a subject of considerable importance (see Cvitanovic et al. 2013).

In addition to their goal as fisheries management tools, NTMRs are increasingly promoted as a strategy for enhancing coral reef resilience through indirect effects (Almany et al. 2009, Botsford et al. 2009, McLeod et al. 2009, McCook et al. 2010, Babcock et al. 2010, Mumby et al. 2014, Olds et al. 2014, Mellin et al. 2016, Roberts et al. 2017). Resilience can be defined as the ability for an ecosystem to withstand shocks of natural and anthropogenic origin, continually resisting the transition into unstable or alternative states, and reassembling following disturbance (Folke et al. 2004, Nyström et al. 2000, Hughes et al. 2003, Gunderson and Pritchard 2012). By conserving coral reef ecosystem processes, through sustaining diverse and abundant coral and fish assemblages, and retaining trophic interactions prior to disturbances or threats, NTMRs may create a buffer against chronic stresses, or enhance recovery following acute impacts (see for e.g. Green et al. 2014, Graham et al. 2015, Mellin et al. 2016, Roberts et al. 2017). But resilience is inherently difficult to assess, and evidence for NTMRs promoting coral reef resilience remains equivocal (Babcock et al. 2010, Halpern et al. 2013, Emslie et al. 2015, Mellin et al. 2016, Wenger et al. 2015, Roberts et al. 2017, Bruno et al. 2019).

Chronic and acute threats of poor water quality, pollution, thermal stress, severe storm events and coral predators can compromise coral reef habitat for fishes (Munday et al. 2008, Hoey et al. 2016, Pratchett et al. 2011, Adam et al. 2014), irrespective of NTMR protection (Jones et al. 2004, Halpern et al. 2013, Williamson et al. 2014, Emslie et al. 2015, Russ et al. 2015a, Wenger et al. 2015, Samoilys et al. 2018). For example, poor water quality (e.g. pollutants, sediments and nutrients) coming onto coastal coral reefs from land is now recognised as a considerable threat to coral reefs, and particularly fishes

that rely on live coral cover (e.g. Salvat 1987, Rogers 1990, Babcock and Smith 2002, Fabricius 2005, Jackson et al. 2014, Kroon et al. 2014; 2016, Hamilton et al. 2017). Furthermore, severe climatic disturbances such as cyclones and coral bleaching deplete live hard coral and modify fish assemblages (Bellwood et al. 2006; 2012, Wilson et al. 2006, Pratchett et al. 2008; 2011, Adam et al. 2014, Graham et al. 2015, Samoilys et al. 2018). Site attached, coral dependent species like damselfish and butterflyfish are generally the most acutely impacted by depletion of corals (Jones et al. 2004, Russ and Leahy 2017, Cheal et al. 2008), while the response of larger bodied and highly mobile species is more variable (Jones et al. 2004, Williamson et al. 2014, Emslie et al. 2015). However, groups of fishes that forage on dead reef pavement and coral skeletons may increase in abundance after disturbance-induced coral mortality, at least in the short term (Cheal et al. 2008, Adam et al. 2011, Gilmour et al. 2013, Russ et al. 2015b; 2018, Richardson et al. 2018). Coral reef habitat is undoubtedly an essential resource for coral reef fishes, but understanding the relative roles of habitat, environmental processes and fishing (or NTMR protection) in shaping and maintaining the structure of fish assemblages is central to the way we manage coral reefs.

1.1 Thesis aims and outline

Given the clear importance of coral reef habitat for maintaining fish assemblages, of environmental conditions and disturbance events in shaping the structure and biodiversity of fish assemblages, and of NTMRs in conserving fish assemblages, exploring the interaction and relative importance of these factors is important for improving our ability to adopt management strategies that ensure sustainability of fisheries and conservation of ecosystems. Thus, the overall goal of this thesis was to improve coral reef management capabilities by increasing our understanding of how

NTMRs perform as fisheries management and conservation tools considering the interaction of coral reef benthic and fish assemblages with prevailing environmental and anthropogenic conditions, including severe disturbances. To achieve this goal this thesis had four aims:

(1) Understand the effect of severe environmental disturbances on coral reef fish assemblages that occur along an existing environmental gradient, irrespective of no-take marine reserves;

(2) Understand whether no-take marine reserves remain effective as fisheries management tools irrespective of severe environmental disturbances and environmental variation;

(3) Understand the relative importance of habitat, environmental variation and no-take marine reserves in driving assemblages of coral reef fishes targeted by fishing, and fishes not targeted by fishing;

(4) Understand whether differences in environmental conditions among coral reef sites affect the trophic ecology of important coral reef fishery species.

Each of these aims was addressed in an independent, but complementary study organised into four Chapters, with each consecutive Chapter building on the previous one. Each Chapter corresponds to a manuscript published, submitted, or intended for publication. **Chapter 2** compares changes in coral reef benthic assemblages, and the assemblage structure, biomass and species (trait) richness of assemblages of nominally herbivorous coral reef fish across the continental shelf of Australia's Great Barrier Reef, before and after two cyclones and a severe thermal bleaching event, to understand whether inner-, mid- and outer-shelf assemblages respond differently to disturbance given

their exposure to different environmental conditions. **Chapter 3** uses a similar environmental and disturbance setting in the Philippines to layer in the effect of NTMRs on coral and fish assemblage structure, and fish biomass. Here, I explore whether NTMRs still perform as fisheries management tools by increasing fish biomass relative to fished areas, considering differences in environmental conditions between island types, and also considering the occurrence of typhoon impacts. The environmental gradients in this study compare large, high elevation, "mainland" islands with high human population density, with small, low-lying and relatively uninhabited "offshore" islands. **Chapter 4** builds directly on Chapter 3, by teasing apart the relative importance of coral reef habitat-level characteristics, island-level environmental characteristics, and NTMR characteristics of size and age, in driving the abundance and species richness of fishes targeted, and not targeted, by fishing. This chapter investigates if bottom-up (habitat as a resource of food and shelter) or top-down (predation pressure) processes determine the structure of fish assemblages. This chapter incorporates up to 20 predictor variables across categories of habitat-scale (coral cover, structural complexity, depth etc.), island-scale (island elevation, distance of reef to nearest river, etc.), and NTMR characteristics (size, age, protection status). Having explored the importance of environmental conditions on influencing fish assemblages, I use **Chapter 5** to test whether differences in environmental conditions among and within islands influence food availability for fishes, such that their primary dietary sources change among sites. To do this, I use experimental manipulations to establish environmental differences among sites, combined with stable isotope analysis to trace dietary sources through to fish tissues. Finally, the General Discussion of **Chapter 6** considers how the results of this thesis contribute to our knowledge and application of coral reef ecology towards management.

Chapter 2:

Cross-shelf differences in the response of herbivorous fish assemblages to severe environmental disturbances

2.1 Abstract

Cross-shelf differences in coral reef benthic and fish assemblages are common, yet it is unknown whether these assemblages respond uniformly to environmental disturbances, or whether local conditions result in differential responses of assemblages at different shelf positions. Here, I compare changes in the taxonomic and functional composition, and associated traits, of herbivorous reef fish assemblages across a continental shelf, five years before, and six months after two severe cyclones and a thermal bleaching event that resulted in substantial and widespread loss of live hard coral cover. Each shelf position maintained a distinct taxonomic assemblage of fishes after disturbances, but the assemblages shared fewer species among shelf positions. There was a substantial loss of species richness following disturbances within each shelf position. Total biomass of the herbivorous fish assemblage increased after disturbances on mid- and outer-shelf reefs, but not on inner-shelf reefs. Using trait-based analyses I found there was a loss of trait richness at each shelf position, but trait specialisation and originality increased on inner-shelf reefs. This study highlights the pervasiveness of extreme environmental disturbances on ecological assemblages. Whilst distinct cross-shelf assemblages can remain following environmental disturbances, assemblages have reduced richness, and are potentially more vulnerable to chronic localised stresses.

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2.2 Introduction

Environmental gradients across small spatial scales produce distinct assemblages of species. For example, plant and animal assemblages have been shown to vary with altitudinal gradients (Fu et al. 2006, Blake and Loiselle 2017, Di Musciano et al. 2018), with salinity gradients (Thiel et al. 1995), and with water quality and wave energy gradients (Done 1982, Wilkinson and Cheshire 1988, Williams 1991, Fabricius et al. 2005, De'ath and Fabricius 2010, Neves et al. 2016). Maintaining these spatially distinct species assemblages enhances overall biological and ecological diversity, and contributes to economic and social prosperity (Balmford et al. 2002, Cardinale et al. 2012). While the biophysical drivers that maintain these assemblages over small spatial scales are increasingly understood, we do not fully appreciate how distinct assemblages along environmental gradients respond to environmental disturbances. This is concerning because many species, habitats and assemblages occur at the extremes of environmental gradients, making them more vulnerable to change (Pianka 1974). This is particularly pertinent to tropical coral reefs spanning continental shelves.

Differences in assemblages of species across continental shelves produce some of the most pronounced spatial variability among coral reefs. Indeed, cross-shelf differences in species abundance and community structure are often more distinct than latitudinal or temporal differences (Done 1982, Williams and Hatcher 1983, Williams et al. 1986, Mapstone et al. 1998, Cheal et al. 2012). Environmental gradients of improving water quality, and increasing wave energy contribute to the distinct assemblages of corals, algae and fishes on inner-, mid- and outer-shelf reefs of Australia's Great Barrier Reef (Done 1982, Williams and Hatcher 1983, Williams et al. 1986, Mapstone et al. 1998, Bellwood and Wainwright 2001, Fabricius et al. 2005, Wismer et al. 2009, De'ath and Fabricius

2010, Emslie et al. 2010, Cheal et al. 2013, Johnson et al. 2019). Nearshore, or inner-shelf, reef habitats are typically characterised by sediment tolerant coral species and morphologies such as massive Porites, and high cover of macroalgae such as *Sargassum* (Fabricius et al. 2005, Hoey and Bellwood 2010). In contrast, outer-shelf reef habitats are generally characterised by higher coral cover but low macroalgal cover (Done 1982, Williams et al. 1986, Wismer et al. 2009). These environmental and habitat characteristics lead to distinct cross-shelf differences in coral reef fish assemblages.

Coral reefs are becoming increasingly subjected to a wide range of environmental stressors. Localised environmental disturbances (e.g., terrigenous runoff), and more spatially extensive disturbances (e.g., thermal stress and severe cyclones) are intensifying with climate change (Hughes et al. 2017). Such disturbances potentially threaten the distinct patterns of coral reef assemblages across continental shelves. Thermal bleaching events can cause widespread loss of live coral cover, while severe tropical storms can remove both live coral cover and the underlying physical structure, leading to the loss of taxa that are dependent on live coral and/or the physical structure that they provide (Wilson et al. 2006). While many reef fish species experience deleterious effects of environmental disturbances that cause benthic habitat change, others can benefit from such habitat change, at least in the short term (Wilson et al. 2006, Adam et al. 2011, Pratchett et al. 2011, Russ et al. 2015; 2018). Coral reefs subject to severe environmental disturbances often become more suitable to rubble specialists like some damselfishes (Pomacentridae), goatfishes (Mullidae) and wrasses (Labridae), and those fish that feed on algae or utilize hard reef pavement platforms, such as nominally herbivorous parrotfishes (Scarinae) and surgeonfishes (Acanthuridae) (Jones et al. 2004, Bellwood et al. 2006, Pratchett et al. 2011, Bellwood et al. 2012, Russ et al. 2015; 2018, Hoey et al.

2016). However, if environmental disturbances are large enough to affect coral reefs across entire continental shelves, it is not known whether local environmental conditions at each shelf position continue to maintain distinct assemblages post disturbance, or whether severe environmental disturbances reduce or even eliminate differences in cross-shelf assemblages.

Herbivorous reef fishes are a critical group that through their feeding activities help maintain a healthy balance between corals and macroalgae (Bellwood et al. 2006, Mumby et al. 2006). Cross-shelf assemblages of herbivorous reef fishes are often distinct in taxonomic structure (Russ 1984, Hoey and Bellwood 2008, Emslie et al. 2012, Cheal et al. 2013, Hoey et al. 2013; 2016, Johnson et al. 2019), as well as being highly diverse in diet, feeding mode and behaviour (Green and Bellwood 2009), often collectively referred to as 'function' (but see Bellwood et al. 2019). Nominally herbivorous reef fishes are typically categorised into two groups based on the substrata they bite; macroalgal 'browsers' that typically bite erect or fleshy macroalgae, and 'grazers' that bite surfaces covered with algal turfs and associated infauna and microbes. Within grazers, groups can be further described as scrapers, excavators, algal croppers and detrital feeders, based on jaw morphology and observed feeding behaviour (Green and Bellwood 2009). Macroalgal browsers have the capacity to remove macroalgal biomass (Streit et al. 2015), scrapers and excavators contribute to the turn-over and distribution of carbonate in coral reef systems (bioerosion) (in Hoey and Bonaldo 2018) while targeting protein-rich epilithic and endolithic micro-organisms (Clements et al. 2016), and algal croppers and detrital feeders contribute to the turn-over of productivity on coral reefs (Williams et al. 1986, Hatcher 1988). Such diversity and functional variation of herbivorous fishes may allow for rapid detection of ecosystem change through trait-based approaches that capture

more nuanced variation than approaches based on broad functional groupings alone (Mouillot et al. 2013). However, it remains unknown how cross-shelf differences in diversity (be it taxonomic, trait or functional) are affected by shelf-wide environmental disturbances, and thus, what the implications are for maintenance of trophic interactions.

Given the widespread distribution and importance of herbivorous fishes to coral reefs globally, this study investigates the response of assemblages of herbivorous reef fish across a continental shelf gradient to severe environmental disturbance events. Specifically, I sought to understand 1. the cross-shelf variation in benthic cover, and herbivorous fish assemblage structure five years before, and six months after two severe cyclones and a severe bleaching event, 2. the overall impact of severe environmental disturbances on the taxonomic and trait-based composition, and biomass of herbivorous fish across the continental shelf, 3. whether inner-, mid- and outer-shelf benthic and reef fish assemblages respond differently to environmental disturbance events given the differences in prevailing local environmental conditions at each shelf position. I then discuss the potential of recovery for inner-, mid- or outer-shelf coral reef assemblages, considering local environmental conditions.

2.3 Materials and methods

2.3.1. Study area

This study took place in the northern section of the Great Barrier Reef (approx. 14°41'S, 145°27'E). Six coral reefs were selected to span the continental shelf including two inner-shelf reefs (located in the Turtle Island Group), two mid-shelf reefs (Lizard Island and MacGillivray reef), and two outer-shelf reefs (Hicks and Day reefs) (Figure 2.1). Within each of these six reefs, the reef crest habitat was selected to compare cross-shelf

changes in benthic biota, and herbivorous fish species, before and after the impacts of two category 4 cyclones (Ita – April 2014, and Nathan – March 2015), and a severe coral bleaching event (March–April 2016) (Hughes et al. 2017, Gordon et al. 2018). Benthic and herbivorous fish assemblages were surveyed twice at all reefs, once approximately five years 'before' the first disturbance event in the Austral summer of 2008/09, and once 6 months 'after' the last disturbance event, in October-November 2016.

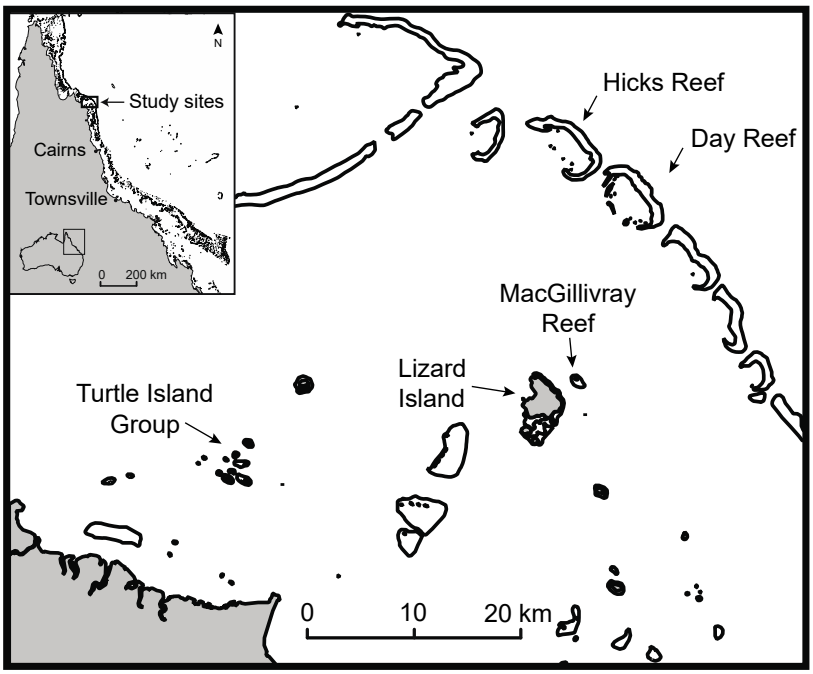

Figure 2.1. Map of the study area (modified from Hoey and Bellwood 2010).

2.3.2 Assessment of benthic and fish assemblages

The benthic assemblage was assessed along point-intercept transects at each reef, both before (Dec 2008-Jan 2009: A. Hoey – all sites) and after disturbances (Oct-Nov 2016: A. Hoey – Turtle Island Group sites, L. Richardson – Hicks and Day Reefs sites, A. Graba-Landry – Lizard Island and MacGillivray Reef sites). In 2008/9, benthic composition was quantified along six replicate 10 metre transects at each of two sites on each of the six reefs. The substratum immediately under, and one meter either side of a transect tape,

was recorded at 1 m intervals (following (Hoey and Bellwood 2010)). In 2016, benthic composition was quantified along four replicate 50 m transects at each site, with the substratum immediately under the transect recorded at 50 cm intervals (following Hoey et al. 2011). Both benthic surveys used point-intercept methods, and haphazard placement of transects within each site, and as such the estimates from the different benthic survey methods should be comparable. Benthic categories were recorded as sand, rubble, dead coral, reef pavement, live hard coral, soft coral, macroalgae, or 'other' benthic organisms. Hard coral was identified to the highest taxonomic classification possible (usually genus), and further categorized by life forms of massive, branching, tabulate, digitate, encrusting and foliose. Algae was identified to genus where possible, but otherwise classified as fleshy macroalgae, filamentous turf algae, or calcareous. Transects were standardized by expressing each benthic category as a percent benthic cover.

The abundance of all diurnally active, nominally herbivorous roving fishes (Families Acanthuridae, Ephippidae, Kyphosidae, Siganidae, and subfamily Scarinae (in Labridae) excluding *Bolbometopon muricatum* due to the highly mobile and aggregated nature of this species), were recorded at each of the 12 sites, in both years. In 2009, the surveyor (A. Hoey) performed four replicate 10-minute timed swim transects at each site, counting all herbivorous fishes greater than 10 cm total length (TL) within a 5 m belt along the reef crest, from the benthos to the water's surface, following Hoey and Bellwood (2010). The length covered by each transect was, on average, 117 m (± 27.7 SE). In 2016, the surveyors (A. Hoey – Turtle Island Group sites, E. McClure, remaining sites) performed four replicate 50 m x 5 m belt transects, following Hoey et al. (2011), whereby a transect tape was simultaneously laid while surveying to reduce any potential diver-related disturbance to fishes. The two fish census methods employed in this study to collect data

before (2008/2009) and after (2016) environmental disturbances are considered comparable to one another. They have similar diver effects on fish, in contrast to methods that lay transect tapes prior to survey, which are more likely to impact accuracy of fish density estimates (Dickens et al. 2011). Furthermore, the width of transects was the same between years (5 m), and the difference in distance covered by each survey method is comparable to previous studies that found no effect on the detectability of fishes when transect lengths varied from 110 to 400 m (Bellwood and Wainwright 2001). In both years, fish were identified to species level, and placed into 5 cm length categories. Abundance estimates were converted to biomass using published species length-weight relationships (Kulbicki et al. 2005) and standardized per hectare (kg ha^{-1}). Species were categorized into functional groups, based on their diet (and/or feeding substrata) and feeding mode (Choat et al. 2002, Green and Bellwood 2009, Pratchett et al. 2011, Froese and Pauly 2018). In this study, the term "function" is used to refer to the process of feeding of a species rather than any ecological "service" provided by that feeding process (Kiørboe et al. 2018, Bellwood et al. 2019).

Species traits are often used as a proxy for their function, however direct links between traits and function are rarely established (see Kiørboe et al. 2018, Bellwood et al. 2019). To assess cross-shelf differences in the trait structure of roving herbivore assemblages in 2008/9 and 2016, all surveyed species were classified according to six traits: diet (macroalgal browsers, scrapers, excavators, algal croppers, detritivores, omnivores) maximum reported body-size (TL, 10 cm size classes), social grouping, position in the water column, mobility within/between reefs, and time of activity (diurnal, nocturnal) based on published literature (Green and Bellwood 2009, Froese and Pauly 2017, Pratchett et al. 2011) (Table S2.1).

2.3.3. Statistical analyses

Cross-shelf differences in the taxonomic composition of herbivorous fish assemblages were assessed across years using a PERMANOVA (maximum permutations = 9999), with shelf position and year (fixed), and site (random, nested in shelf) as factors, and potential interactions among shelf position and year included. Monte Carlo sampling was used when there were insufficient unique permutations for P-value estimation (<100 permutations (Clarke and Warwick 2001)). These differences were then visualised using a non-metric multidimensional scaling (nMDS) based on Bray-Curtis similarity of data at the transect level. Percentage similarity analysis (SIMPER) was used to identify the mean similarity within, and dissimilarity among herbivore assemblages found in the inner-, mid-, and outer shelf in each year, and species identified that consistently contributed to within group similarity (with similarity/SD ratio ≥2, Table S2.2) (Clarke and Warwick 2001). This was supported by multivariate dispersion analysis (MVDISP) to quantify differences in assemblage composition both within and among shelf groups in 2008/9 and 2016. Cross-shelf variation in species dominance patterns across years was tested with a two-way crossed analysis of similarity (ANOSIM) using shelf position and year as fixed factors, based on a dissimilarity matrix of log-weighted species rank (with DOMDIS). Pairwise comparisons of species dominance over time (pre and post-disturbance) were assessed within each individual shelf position. All multivariate analyses were performed on fourth root transformed transect level data.

Linear mixed-effects models were used to assess cross-shelf differences in total cover of coral (hard coral and *Millepora* spp.) and macroalgae over time, and the trait structure of herbivorous fish assemblages (trait richness; trait specialisation; trait originality; total log transformed herbivore biomass; and biomass of individual functional groups: browsers,

croppers, scrapers, detrital feeders, excavators) and taxonomic diversity (Shannon diversity, H) over time. All models included shelf position, year, and their interaction (fixed effects), and site (random effect), fit within a Gaussian structure due to normal residual distributions, followed by planned comparisons (if interaction detected) or Tukey multiple comparisons (no interaction) post hoc to identify where differences occurred. Model assumptions of homogeneity of variance, normality, and independence were validated with visual assessments of Pearson residual diagnostic plots. Where heterogeneity of variance occurred among shelf positions (total cover of macroalgae, log transformed total herbivore biomass, biomass of each herbivore functional group, trait specialisation, and trait originality), or across years (total hard coral cover), models were fitted with a constant variance structure.

The trait richness of the herbivorous fish assemblages was calculated for each transect by constructing a principal coordinates analysis (PCoA) of species positioned in multidimensional trait-space based on a Gower distance matrix of species pairs, and a square root correction for negative eigenvectors (Legendre and Legendre 1998). Scores from the first four PCoA axes summarising species distributions in trait-space were combined with species biomass to calculate three complementary indices of trait diversity: trait richness, trait specialisation, and trait originality (Mouillot et al. 2013, Maire et al. 2015). Trait richness represents the range of unique trait entities and is calculated as the proportional convex hull volume occupied by species present in the trait-space. The average trait specialisation of an assemblage (i.e. species close to the periphery of trait space) was calculated as the biomass-weighted relative distance of a species from the centroid of trait-space. Trait originality indicates the isolation of species in trait-space and is calculated as the mean pairwise distance of biomass-weighted species

present. Three transects were omitted for calculation of trait diversity (from 2016 surveys of site Turtle North 1) due to minimum trait entity requirements to compute convex hulls.

Multivariate analyses of the taxonomic composition of herbivore assemblages were performed in Primer v6 with PERMANOVA+ (Clarke and Warwick 2001, Anderson et al. 2008). All other analyses were performed in R (R Core Team 2008), with the packages *lme4, nlme, multcomp, MumIn, ape, cluster, geometry, rcdd, vegan, ade4,* and *FD* (*FDchange*).

2.4. Results

The best model of total hard coral cover included shelf position, year, and their interaction. Total hard coral cover was highest on outer-shelf reefs, and lowest on inner-shelf reefs in both 2008/9 and 2016 (Fig. 2.2a). Macroalgal cover was highest on inner-shelf reefs and almost non-existent on mid- and outer-shelf reefs (Fig. 2.2b). These patterns did not change with environmental disturbance, despite significant declines in hard coral cover across the shelf, and significant increases in macroalgal cover on the inner shelf (Fig. 2.2, Table S2.3).

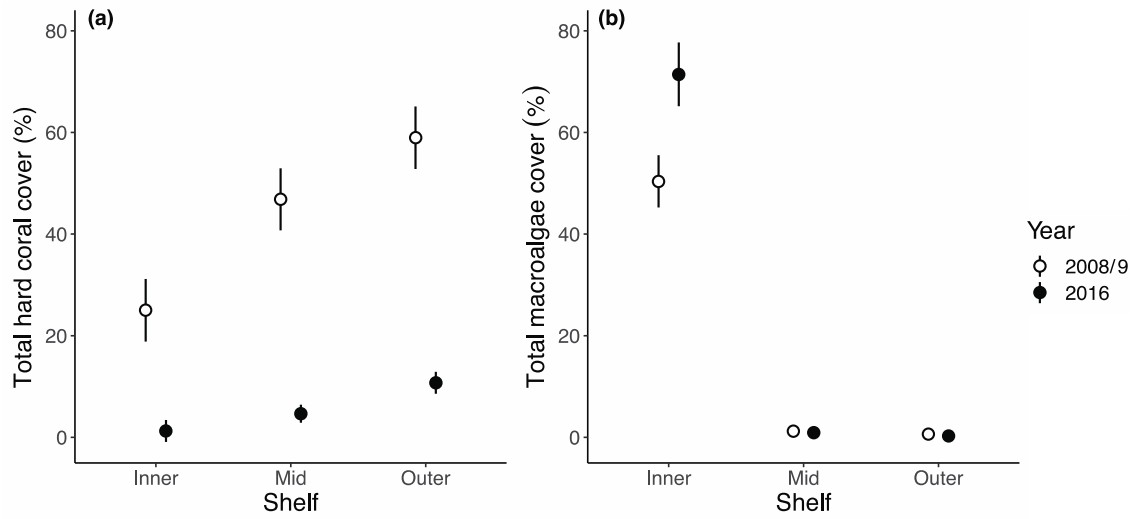

Figure 2.2. Cross-shelf differences (fitted values 95% confidence intervals) in: (a) total hard coral cover (%), and (b) total macroalgal cover (%) in 2008/9 (white) and 2016 (black).

Assemblage structure of herbivorous reef fish was distinct among shelf positions both before and after environmental disturbances (PERMANOVA, Pseudo-F = 3.86, df = 2, 65, P = 0.001, unique permutations = 9950, Fig. 2.3, Table S2.2). Assemblage structure changed at all shelf positions following disturbances, and significantly so on the inner and outer shelf (PERMANOVA, pairwise comparisons: both P = 0.03). Following disturbances, fish assemblages became more distinct among shelf positions, but more variable within shelf positions, with environmental disturbances increasing the cross-shelf assemblage differences in multivariate space (Fig. 2.3, Table S2.2). Across the shelf, increased assemblage differences were characterised by a marked decrease in species richness at all shelf positions (ANOSIM, Inner: Global-R = 0.82, P = 0.03, Mid: Global-R = 0.90, P = 0.005, Outer: Global-R = 0.99, P = 0.03). On inner-shelf reefs four characteristic species decreased to one (*Scarus rivulatus*), on mid-shelf reefs eight characteristic species decreased to one (*Acanthurus nigrofuscus*), and on outer-shelf reefs eight characteristic species decreased to two (*Acanthurus lineatus* and *Ctenochaetus striatus*) (SIMPER: simm/SD ≥2, Table S2.2).

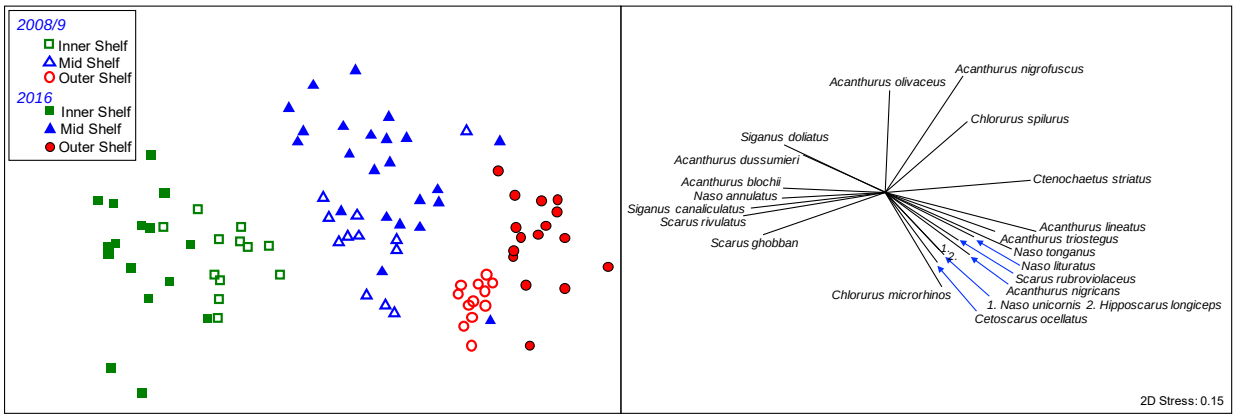

Figure 2.3. Non-metric multidimensional scaling analysis showing cross-shelf differences in assemblage structure of herbivorous reef fishes (green square: inner-, blue triangle: mid-, red circle: outer-shelf) in 2008/9 (open) and 2016 (filled), using transect-level fourth root transformed data. The relative contributions of species to the observed variation in composition are illustrated (>0.4 Pearson correlation).

Prior to environmental disturbance, total biomass of all roving herbivorous fishes was highest on outer-shelf reefs, and not significantly different between mid- and inner-shelf reefs. Following disturbances, total biomass increased significantly on mid- and outer-shelf reefs but did not change significantly on inner-shelf reefs (Fig. 2.4a, Table S2.3). Increased biomass on the mid- and outer-shelf reefs was driven by significant increases in biomass of algal croppers and detrital feeders (Fig. 2.4b, c, Table S2.3). Concurrently, there were slight declines in biomass of excavators, macroalgal browsers, and scrapers across the shelf (Fig. 2.4d, e and f, Table S2.3).

The four PCoA axes used to describe fish species distribution in trait-space cumulatively explained 61.23% of the variability. Analysis of cross-shelf variation in the assemblage structure of herbivorous fishes revealed changes in taxonomic (Shannon, H, and total log

biomass) and trait characteristics (trait richness, specialisation, and originality) in response to disturbances. However, the nature and extent of the changes varied with metric and, in some instances, with shelf position (Fig. 2.5, Table S2.3). Trait richness (Fig. 2.5a) and taxonomic diversity (Shannon, H) (Table S2.3) declined significantly across the entire shelf following disturbance. However, patterns of cross-shelf differences in both metrics were maintained, with greater trait richness and taxonomic diversity (H) of assemblages on the mid-shelf than the inner- and outer-shelf reefs in both 2008/9 and 2016 (Fig. 2.5, Table S2.3).

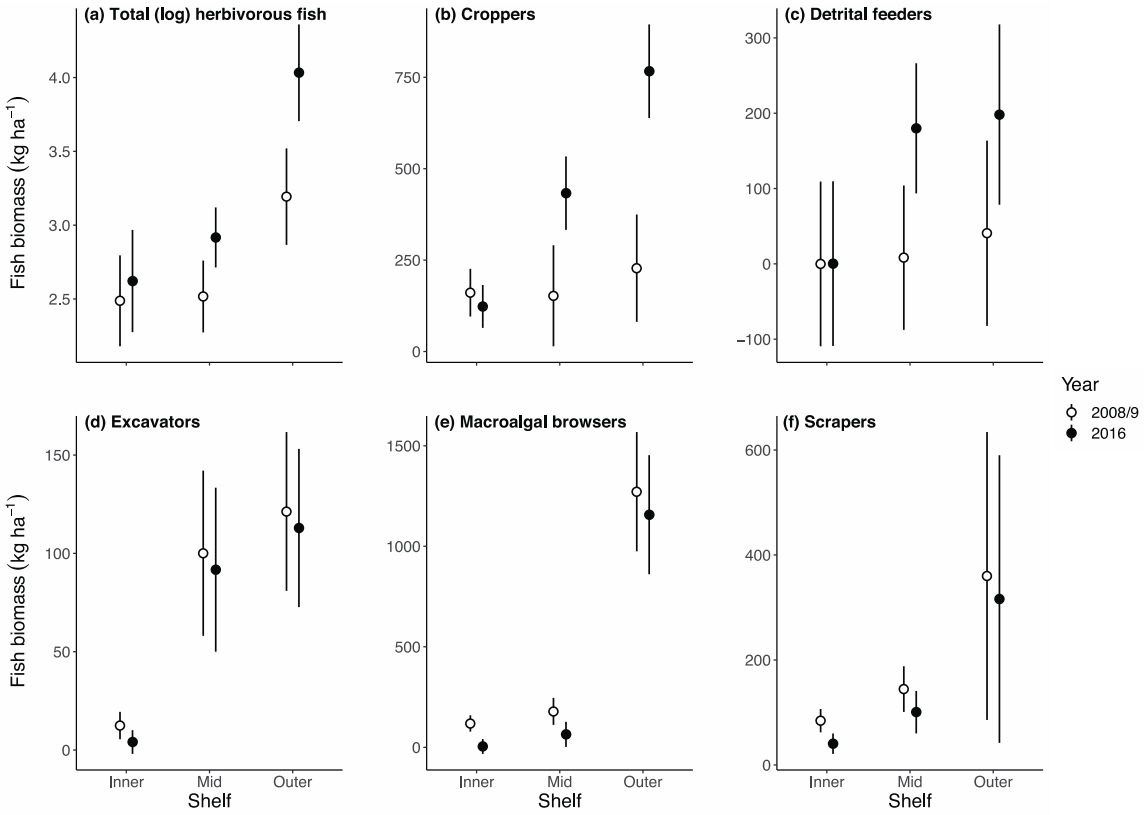

Figure 2.4. Cross-shelf differences (fitted values 95% confidence intervals) in biomass (kg/ha) of: (a) total herbivorous fishes (log transformed), (b) algal croppers, (c) detrital feeders, (d) excavators (less *Bolbometopon*), (e) macroalgal browsers, and (f) scrapers, in 2008/9 (white) and 2016 (black).

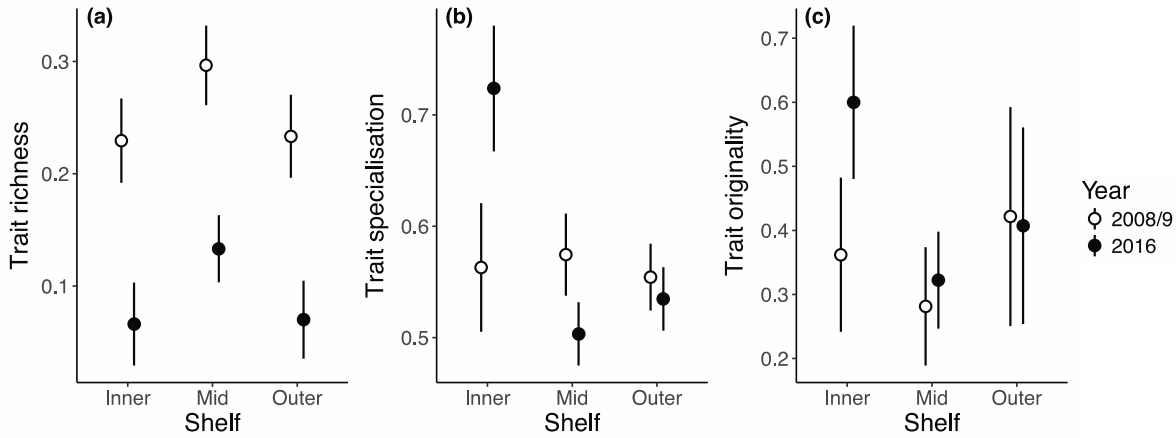

Figure 2.5. Cross-shelf differences (fitted values 95% confidence intervals) in: (a) trait richness, (b) trait specialisation, and (c) trait originality, in 2008/9 (white) and 2016 (black).

Responses to environmental disturbance in trait specialisation and originality of herbivore assemblage structure did vary with shelf position. Trait specialisation and originality of herbivore assemblages increased significantly on the inner shelf, indicating an increase in biomass of 'specialist' species positions towards the periphery of trait space, and a potential loss of redundancy, respectively (Fig. 2.5, Table S2.3). Conversely, the trait specialisation of assemblages decreased on the mid-shelf reefs indicating a loss of biomass of 'specialist' species. Neither trait specialisation nor originality of assemblages changed on outer-shelf reefs with disturbance (Fig. 2.5, Table S2.3).

2.5. Discussion

To date, no other study has explored how coral reef assemblages across a continental shelf gradient respond to severe environmental disturbances that affect each shelf position similarly. This study found that severe cyclonic and thermal impacts caused substantial loss of live hard coral cover and caused significant loss of taxonomic diversity of herbivorous reef fish assemblages across the continental shelf in the northern GBR. Prior

to disturbances, there were clear differences in the taxonomic composition of roving herbivore assemblages at each shelf position. Following disturbances and loss of species richness, distinctness in shelf assemblages increased, particularly on the outer- and inner-shelf, as assemblages became less similar in their species composition. This was caused by reductions in species richness at each shelf position that resulted in dominance of biomass by a few species and functional groups common at each shelf position. The biomass of these new dominant species increased substantially on the mid- and outer-shelf reefs, enough to override biomass loss caused by reductions of other species. The biomass of herbivorous fish on the inner-shelf reefs remained stable at pre-disturbance levels, however the inner-shelf reefs had a reshuffling of species dominance to become characterised by a different suite of species following disturbance. There were significant losses of trait richness at all shelf positions. Inner-shelf reefs were the least diverse, in both species and traits, of any shelf position prior to disturbance, and appear the most vulnerable to a potential loss of redundancy, as evidenced by significant increases in trait originality and trait specialisation post-disturbance. This is particularly concerning since inner-shelf reefs are arguably subject to greater localised environmental impacts of increased sedimentation and runoff from terrestrial sources than mid- and outer-shelf reefs. Potential loss of redundancy of this important group of fishes, and increased cover of macroalgae and poor water quality, may make it more difficult for these reefs to recover, especially considering increasing threats of pervasive climate change.

Cross-shelf differences in the response of herbivorous fishes to disturbance may suggest differential susceptibility of each shelf position to disturbances. This may be influenced by the prevailing cross-shelf gradients of water-quality, particularly on inshore reefs (Williams et al. 1986, Fabricius et al. 2005, Cheal et al. 2013), together with increasing

wave action (Wilkinson and Cheshire 1988) and upwelling (Andrews and Gentien 1982), particularly on outer- and mid-shelf reefs. That the inner-shelf herbivorous fish assemblage showed the lowest species richness and trait richness before disturbance, and particularly after disturbance, may indicate that inner-shelf reefs are particularly susceptible to environmental disturbances (also see Cheal et al. 2013). However, cross-shelf differences among inner-, mid- and outer-shelf herbivorous fish assemblages became more pronounced following disturbance, with all shelf assemblages becoming less similar to each other, diverging towards greater dominance by fewer species, and greater within-shelf variability in the occurrence of species. This reduced richness of herbivorous fish within shelf positions, and increased difference in assemblages of herbivorous fish among shelf positions suggests that maintenance of ecosystem structure across the shelf may be difficult in light of predicted increases in environmental disturbance regimes (Hughes et al. 2017, Richardson et al. 2018).

Despite relatively uniform loss of species richness across the shelf, the biomass of all herbivores increased on mid- and outer-shelf reefs, but not on inshore reefs. This was driven largely by an increase in biomass of algal croppers and detrital feeding reef fish on mid- and outer-shelf reefs. Following disturbance, inner-shelf reefs became characterised by *Scarus rivulatus* (a scraper), mid-shelf reefs became characterised by *Acanthurus nigrofuscus*, and outer-shelf reefs became characterised by *Acanthurus lineatus* and *Ctenochaetus striatus*. Increasingly we are seeing herbivorous fish assemblages respond differently to disturbance events compared to many other trophic groups (see Russ et al. 2018). Typically, substantial loss of live hard coral cover and structure following environmental disturbances, leads to a severe loss of coral dependent species (Jones et al. 2004, Wilson et al. 2006, Pratchett et al. 2011; 2014). This may include juveniles of

some herbivorous reef fish species that are reliant on live branching corals on inshore reefs for part of their life cycle (eg. Hamilton et al. 2017). However, adults of nominally herbivorous roving species favour feeding over dead coral surfaces and may increase in abundance, biomass and/or growth rate when coral cover is reduced, at least in the short term (Hart and Russ 1996, Adam et al. 2011, Gilmour et al. 2013, Lamy et al. 2015, Russ et al. 2015). This may reinforce the importance of bottom up processes in shaping fish assemblages (Russ et al. 2015; 2018). On the GBR, herbivorous fish are generally not targeted by fishers (Cheal et al. 2013), nor do they respond measurably to management zoning (see Rizzari et al. 2015). Thus, findings of this study compliment and contrast with recent evidence for bottom up responses of fish assemblages following disturbance events, by providing evidence of the simultaneous response of cross-shelf herbivorous fish assemblages to disturbance, for the first time.

Inner-shelf reefs showed the most distinct, and possibly the most concerning response of the assemblages of herbivorous fish to disturbance. While total herbivorous fish biomass was maintained on inner-shelf reefs, trait specialisation and trait originality of the assemblage increased, indicating an increase in biomass of more 'specialist' species, and a potential loss of redundancy, respectively. A loss of redundancy of traits within an assemblage reflects a reduction in the number of species contributing to particular traits, and may affect the maintenance of ecological processes and thus ecosystem persistence (see Folke et al. 2004, Cheal et al. 2013). The differential response of inner- vs mid- and outer-shelf reefs may be due to local environmental conditions (e.g., elevated sediments and nutrients, reduced wave action), or the distinct herbivorous fish assemblages that are more sensitive to habitat disturbance or loss. For example, the greater impact of the disturbances on the inner-shelf reef assemblages may be related to the naturally lower

coral cover and taxonomic richness of assemblages in general (Fabricius et al. 2005). Nevertheless, the potential loss of redundancy on these inner-shelf reefs is concerning since they are the most vulnerable to anthropogenic stressors.

Whilst frequent environmental disturbances are known to cause declines in coral cover and coral-dependent taxa, there is increasing evidence that such disturbances do not similarly impact macroalgal cover. For example, in the Caribbean, assemblages of the macroalgae *Sargassum* recovered to pre-disturbance levels one year post storm disturbance (Engelen et al. 2005). Similarly, on the GBR, *Sargassum* may be able to benefit from disturbance events via rapid growth from holdfasts, colonization of new space through dispersion of propagules and unpalatability of the whole plant for most species of herbivorous fishes (Loffler et al. 2018). Here I show that inner-shelf reefs experienced a significant increase in macroalgal cover following environmental disturbances (including but not limited to *Sargassum*). The loss of redundancy in the herbivorous fish assemblage on inner shelf reefs of the GBR where macroalgae is abundant, including loss of fish species that can remove the biomass of some macroalgal species, combined with the increase in biomass and persistence of macroalgae following disturbances, may enhance both the recovery and spread of macroalgae on these inshore reefs. This may in turn hinder coral recovery (Hughes et al. 2007, Clements et al. 2018) and consequently the recovery of coral-associated fishes. The inner shelf reefs post-disturbance may therefore show a greatly different trajectory of recovery to that of mid- and outer-shelf reefs, where turf algae dominates post-disturbance benthic communities and does not similarly prevent coral recruitment and growth.

That cross-shelf structure of roving herbivorous fish assemblages was distinct at each shelf position prior to disturbances is consistent with previous studies on the GBR (Williams and Hatcher 1983, Russ 1984, Wilkinson and Cheshire 1988, Hoey and Bellwood 2008, Wismer et al. 2009, Cheal et al. 2013, Hoey et al. 2013, Johnson et al. 2019). The differences in assemblage structure of herbivorous fish among shelf positions are likely driven by the natural variation in environmental conditions across the shelf forming distinct habitats that favour particular species (Done 1982, Wilkinson and Cheshire 1988, Cheal et al. 2013). These conditions include higher exposure to terrigenous sediment and nutrient fluxes inshore (Fabricius et al. 2005), and frequent perturbation from high wave energy on outer-shelf reefs (Done 1982, Bellwood and Wainwright 2001), as well as differential settlement habitats, potential variation in the supply of larvae (Williams et al. 1986), and predation pressure (Newman and Williams 1996, Newman et al. 1997, Gust et al. 2002). As herbivorous fishes are not generally targeted by fishers on the GBR (De'ath and Fabricius 2010, Cheal et al. 2013) (some limited recreational spearfishing occurs (Frisch et al. 2008)), fishing is unlikely to influence differences in assemblage structure of herbivorous fishes across the shelf (Cheal et al. 2013). Biophysical factors other than cyclones and bleaching that likely influence differences in assemblage structure cross-shelf (e.g. terrestrial runoff of sediments and nutrients, wave energy) may have varied during this study, and their potential effects should not be discounted. However, potential change in these other environmental drivers was not quantified here. Nevertheless, this study highlights the importance of extreme environmental disturbances on distinct ecological assemblages at different shelf positions. This study also suggests that inherent conditions that make inner-shelf reefs distinct, may also make them particularly vulnerable to disturbance and perhaps slower to recover. If differences in environmental conditions do cause differential shelf responses

to widespread disturbance events, this will likely manifest most noticeably as the reefs recover. This study assessed coral reef assemblages across the continental shelf just six months after the most recent disturbance event in the series. Thus, it is too soon to allow documentation of the long-term recovery trajectory of each shelf assemblage, both benthos and fish. Likely, benthic and fish assemblages at different shelf positions will remain distinct, but monitoring these different assemblages is necessary, particularly considering predicted climate change scenarios.

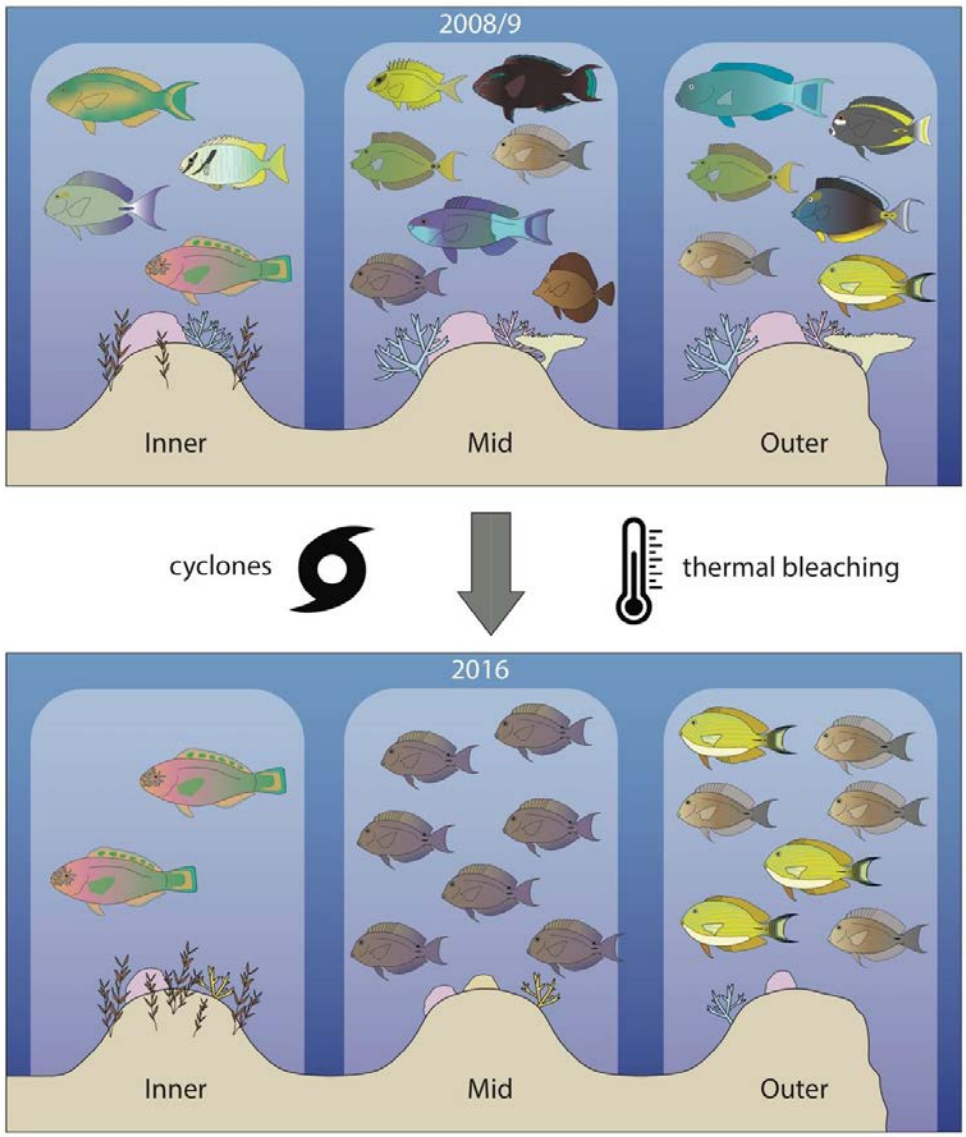

Figure 2.6. Schematic diagram of cross-shelf coral reef and herbivorous fish assemblages before and after cyclone and thermal bleaching disturbance (front cover, *Diversity* 2019: *11*(2))

Chapter 3:

Higher fish biomass inside than outside marine reserves despite typhoon impacts in a complex reefscape

3.1 Abstract

No-take marine reserves (NTMRs) are an important tool for conserving marine biodiversity and managing fisheries. However, with increasing environmental change driven by local and global stressors, it is critical to understand whether NTMRs can continue to provide social, economic and conservation benefits in the long-term. Here, I compare coral reef benthic and fish assemblages across 17 paired NTMR-fished control sites on three heavily populated, high elevation "mainland" islands, and four lowly populated, low elevation "offshore" islands that differed in their exposure to recent typhoons. Neither coral reef benthic assemblages, nor total hard coral cover differed clearly or consistently between NTMR and fished reefs for the same island type and typhoon impact. However, there was less cover of macroalgae in NTMRs than fished areas, most clearly on mainland islands. Typhoons had severe negative effects on live hard coral cover, regardless of island type or NTMR protection. Typhoon-damaged reefs had a different fish assemblage structure, and a lower total biomass of fish, compared to reefs not damaged. Mainland island reefs had a different fish assemblage structure, and a lower total biomass of fish compared to offshore island reefs. NTMRs had a similar fish assemblage structure, and a higher total biomass of fish than fished areas, irrespective of island type or typhoon damage. Despite inherent differences in fish and benthic assemblages between mainland and offshore island coral reefs, NTMRs can provide benefits to fish biomass, even when reefs are affected by typhoons. The development of management strategies that incorporate sound coastal land-use practices, while

positioning NTMRs in areas less prone to typhoon impact, will provide NTMRs the best chance of success if climatic extremes increase.

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3.2 Introduction

Conserving reef fish assemblages is important for both human populations and for the maintenance of coral reef ecosystems. This is especially true in developing island nations where animal protein is often sourced from coastal coral reefs (Cabral and Geronimo 1998), and most reef fish species are targeted by fishing (Berkes 2001). One of the most common community-based management strategies aimed at sustainable use and conservation of marine resources is the implementation of no-take marine reserves (NTMRs), where extractive practices like fishing are prohibited (Lubchenco et al. 2003). NTMRs aim to increase biomass of targeted fish stocks inside (Polunin and Roberts 1993, Russ et al. 2004), and eventually outside NTMR boundaries (McClanahan and Mangi 2000, Abesamis and Russ 2005, Russ and Alcala 2011). While NTMRs are effective in excluding fishing when compliance is maintained (Bergseth et al. 2015), and can support fisheries and conserve biodiversity, studies have shown that NTMRs cannot exclude direct damage to reefs from environmental and climatic threats (Jones et al. 2004). Yet, recent opinion remains divided on whether NTMRs might (Roberts et al. 2017), or might not (Bruno et al. 2019), ameliorate damage caused to coral reefs by climate change. It is suggested that removal of one anthropogenic stress (i.e., fishing) within protected areas may increase the resilience of reefs to other disturbances by maintaining ecosystem

structure (see Roberts et al. 2017). Thus, understanding whether NTMRs can remain effective in their role as fisheries management and conservation tools under increasing environmental disturbance regimes is a priority.

Both chronic stress (e.g. coastal pollution, sedimentation) and acute disturbances (e.g. extreme weather events) have the potential to change coral reef benthic assemblages (Fabricius 2005, Hoey et al. 2016). Such benthic disturbance alters fish assemblages by affecting availability of food and shelter (Wilson et al. 2006, Pratchett et al. 2011). For instance, excessive runoff of sediments and nutrients from land onto nearby reefs can cause coral mortality (Fabricius 2005, Weber et al. 2012), degrade fish nursery habitat (Hamilton et al. 2017) and modify populations of coral dependent fishes (Williamson et al. 2014). Severe tropical storms (cyclones, typhoons, hurricanes) physically break up reefs, removing live coral cover and reef complexity, and reducing populations of fishes that rely on corals for survival (Jones et al. 2004, Pratchett et al. 2011, Russ and Leahy 2017). Conversely, an increase in cover of reef pavement and dead coral skeletons following disturbances, may increase the density of fish groups that preferentially forage on dead coral surfaces such as parrotfish (Russ et al. 2015, Adam et al. 2011), algal farming damselfish (Richardson et al. 2018), and detritivorous surgeonfish (Russ et al. 2018). Evidence of NTMR success in supporting reef ecosystems and fisheries in the face of chronic or acute environmental stress is equivocal (see Emslie et al. 2015, Huijbers et al. 2015, Wenger et al. 2016, Bruno et al. 2019). Uncertainty surrounding how well NTMRs function as fisheries management and conservation tools under environmental change is concerning, especially considering that NTMRs have been established in a diverse array of tropical coral reef seascapes under a variety of human use patterns and environmental conditions.

Differences in environmental conditions among coral reef locations, including island biogeography or the distance of reefs from shore, are important determinants of the diversity and composition of benthic and fish assemblages (e.g. Wilkinson and Cheshire 1988, Fabricius et al. 2005, Taylor et al. 2015). Local environmental conditions are thus an important factor to consider when assessing the relative success of NTMRs as fisheries management and conservation tools. With high human dependency on coral reef resources, particularly in developing nations, and greater extremes in climate anticipated in the future (Knutson et al. 2010), it is critical to understand how NTMRs will perform under a range of environmental conditions and disturbances (Roberts et al. 2017, Bruno et al. 2019). This study investigated whether community-managed NTMRs remain effective as fisheries management tools across a range of sites that varied in environmental conditions, specifically island type and history of typhoon disturbance. I aimed to: 1) characterize coral reef benthic and fish assemblages among multiple, spatially extensive, paired NTMR-fished sites; and 2) explore the success of NTMRs as fisheries management tools in increasing biomass of large-bodied fish relative to fished areas, in areas with and without typhoon damage and on different island types.

3.3 Materials and Methods

3.3.1 Study sites

This study was conducted in the Central Visayas region of the Philippines, where there is a large concentration of small, community-managed NTMRs, in a variety of environmental settings (Alcala et al. 2008, Weeks et al. 2010). I sampled 16 representative complete no-take marine reserves on coral reefs, and one limited fishing marine reserve (Sumilon Island), (total of 17 NTMRs) and paired adjacent fished

(control) sites, located across 7 islands (Fig. 3.1, Table 3.1). Thirteen sites were located on fringing coral reefs surrounding large, higher elevation (>600 to 2000m) 'mainland' islands, potentially subject to large volumes of surface run-off. Four sites were on coral reefs associated with small, lower elevation (<120m) 'offshore' islands with limited surface run-off. Three of these four offshore islands were located on platform coral reefs (Sumilon, Balicasag, Pamilacan) with the fourth offshore island granitic, and surrounded by fringing coral reefs (Apo). Gross human population is 1 to 3 orders of magnitude higher on mainland than offshore islands (Table 3.1). All NTMRs were community-managed and relatively small, with an average size of 12.75 ha (range 3-40 ha; Alcala et al. 2008). At the time of survey (2016), the average duration of protection of NTMRs was 16.4 years (range 4-30) (Table 3.1). Extensive local consultation was undertaken when selecting NTMRs to ensure voluntary compliance to no-take status as much as possible. Thus, it is assumed that NTMRs were equally well-protected (except where specified, i.e. Sumilon Island). NTMRs were never less than 2km apart, and fished control sites were never greater than 500m from their NTMR. Fished controls had benthic habitat comparable to their NTMRs. Exceptions were NTMR-control pair comparisons at Apo Island and Sumilon Island, due to typhoon impacts sustained in 2011 and 2012 (Table 3.1), and natural variations in benthos around these islands. Typhoon damaged sites (Fig. 3.1; Table 3.1) were identified by studying the path of the 2011, 2012 typhoons (Fig. 3.1), by looking at reef aspect in relation to typhoon direction, and importantly through consultation with local reef managers and users, for each NTMR-fished pair site.

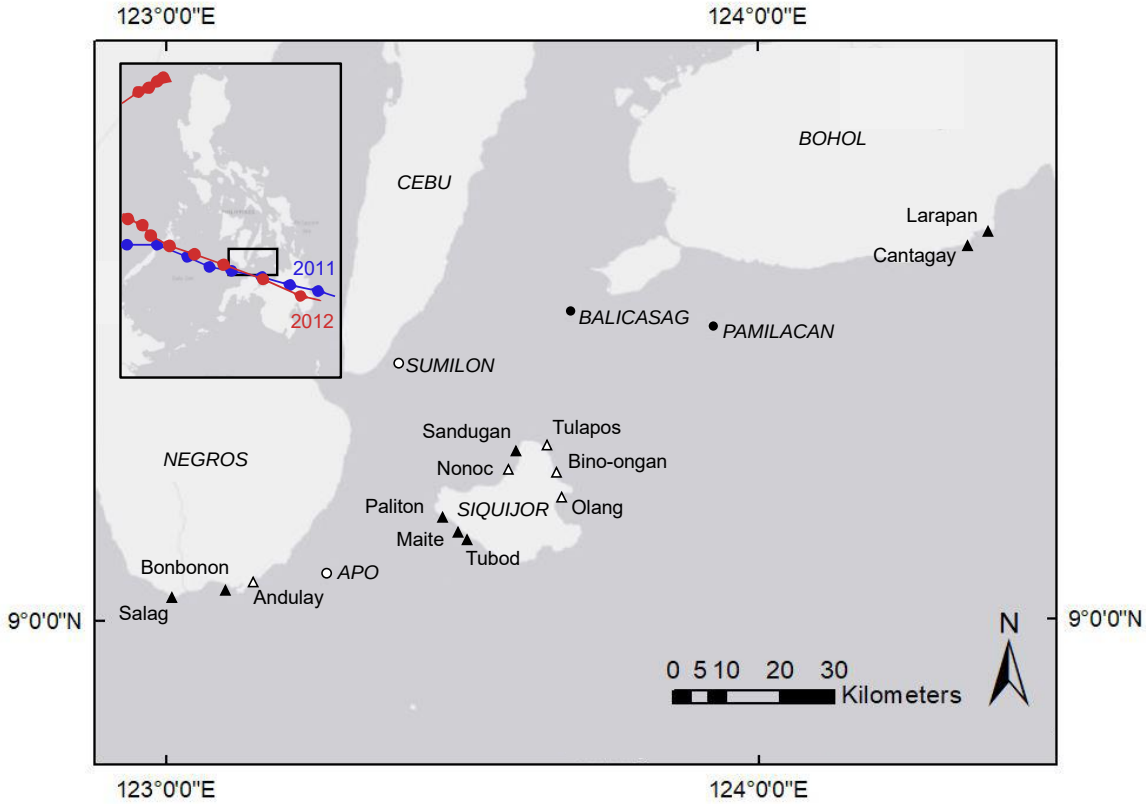

Figure 3.1. Map of the central Philippines showing the location of the 17 NTMR-fished pair sites, on mainland islands (triangles) and offshore islands (circles), including sites unaffected by typhoons (filled symbols) and sites affected by typhoons (open symbols). Inset country map shows the path of typhoons in 2011 and 2012.

3.3.2 Assessment of benthic and fish assemblages

Benthic and fish assemblages were surveyed from May to July 2016, approximately 3.5 years after the most recent typhoon had affected the region (December 2012 – Russ and Leahy 2017). Surveys were performed along three or four 50-metre transects each on the reef crest and reef slope, in both NTMRs and fished areas at each site (229 transects total). Reef crests were sampled at 3-5 m depth, reef slopes at 9-15 m depth. Adjacent transects within each zone were separated by approximately 10 m.

Table 3.1. Details of no-take marine reserves (NTMRs) and paired fished areas surveyed across 7 islands in the central Philippines, with 'Typhoon Damage' applying to both NTMR and fished control sites for any pair, unless otherwise specified. Human population data are available at the level of the municipality, except in the case of Apo and Pamilacan Islands, as indicated by parentheses.

Island	Island Geology	Island Type	Site Name	Location	NTMR Size (ha)	NTMR Age (Years)	Typhoon Damage	Year of Impact	Municipality population
Negros Island	Granitic	Mainland	Salag	9° 2'27"N, 123° 0'30"E	10	15	No	NA	Siaton / 77,696
			Bonbonon	9° 3'0"N, 123° 6'53"E	9	21	No	NA	Siaton / 77,696
			Andulay	9° 3'31"N, 123° 8'21"E	6.4	20	Yes	2011, 2012	Siaton / 77,696
Siquijor Island	Coralline	Mainland	Tubod	9° 8'23"N, 123°30'36"E	8.1	13	No	NA	San Juan / 14,854
			Maite	9° 9'12"N, 123°29'34"E	6.3	7	No	NA	San Juan / 14,854
			Paliton	9°10'26"N, 123°27'28"E	6.5	8	No	NA	San Juan / 14,854
			Nonoc	9°14'32"N, 123°34'22"E	4.13	21	Yes	2011, 2012	Larena / 13,847
			Sandugan	9°17'7"N, 123°35'40"E	10	13	No	NA	Larena / 13,847
			Tulapos	9°17'12"N, 123°38'39"E	27.22	15	Yes	2011, 2012	Enrique Villanueva / 6,104
			Bino-ongan	9°16'21"N, 123°39'8"E	13	4	Yes	2011, 2012	Enrique Villanueva / 6,104
			Olang	9°12'27"N, 123°40'1"E	21.36	14	Yes	2011, 2012	Maria / 13,828
Bohol Island	Granitic	Mainland	Cantigay	9°37'42"N, 124°21'25"E	16.21	15	No	NA	Jagna / 33,892
			Larapan	9°39'5"N, 124°23'39"E	8.24	14	No	NA	Jagna / 33,892
Apo Island	Granitic	Offshore	Apo	9° 4'25"N, 123°16'19"E	15	31	NTMR only	2011, 2012	(Apo) 823
Sumilon Island	Coralline	Offshore	Sumilon	9°25'43"N, 123°23'15"E	40	20	Fished only	2011, 2012	Oslob / uninhabited
Balicasag Island	Coralline	Offshore	Balicasag	9°30'57"N, 123°40'46"E	3.44	18	No	NA	Panglao / uninhabited
Pamilacan	Coralline	Offshore	Pamilacan	9°29'34"N, 123°54'57"E	11.9	30	No	NA	(Pamilacan) 1,418

The number and size of diurnally active, non-cryptic fish species was recorded along each transect, with 314 species from 24 families sampled (Appendix S3.1). The observer (E. McClure) counted larger, mobile fish (>10 cm total length (TL)) within a 5 m wide belt, estimating the length of each individual to the nearest centimetre, while swimming parallel to the contour of the reef and simultaneously laying the transect tape to minimize

disturbance to the fish (following Hoey et al. 2011). Smaller, more site-attached reef fish species (≤10 cm TL), such as damselfishes, small-bodied wrasses, and juveniles of roving adults, were counted within a 2 m wide belt during a return swim along each transect. Lengths of small fishes (≤10 cm TL) were not estimated. Biomass of larger fish was estimated using published length-weight relationships (Kulbicki et al. 2005).

Benthic composition was assessed using the point-intercept method, with benthos immediately under the transect photographed every 50 cm along each transect, and later categorized (K. Sievers). Benthic categories were sand, rubble, epilithic algal matrix (EAM), hard coral, soft coral, macroalgae, and 'other' benthic organisms. Hard coral was further categorised by life forms of branching, tabulate, foliose, massive and encrusting. Algae was categorised as crustose coralline algae (CCA), fleshy macroalgae or turf algae.

3.3.3 Data analysis

Density and biomass of large fish were calculated for each transect of 250 m^2, and density of small fish was calculated for each transect of 100 m^2, and all standardized to 1000 m^2. Permutational multivariate analysis of variance (PERMANOVA), with pair-wise comparisons of factor level, and Monte Carlo simulation for small datasets, were run to statistically test for the effects of typhoon disturbance, island type and NTMR protection, and their interactions, on the benthic and reef fish assemblage structure (all fish density, and large fish (TL >10 cm) biomass). Fish density and biomass were square-root transformed to reduce the contribution of abundant species. nMDS plots based on Bray-Curtis dissimilarity matrices were used to display patterns of benthic and fish species assemblage structure among transects. nMDS with PERMANOVA were performed in PRIMER v6 +Permanova (Anderson et al. 2006).

Generalized linear mixed effects models (GLMMs) were used to assess the effects of typhoon disturbance, island type and NTMR status on the response of "fragile corals" (branching, tabulate, foliose), "robust corals" (massive, encrusting), fleshy macroalgal cover, and large reef fish (>10 cm TL) biomass. GLMMs were run for crest and slope transects separately. All response variables were modelled with a negative binomial distribution and log-link function, with site included as a random factor. The 'best' GLMM models were determined by comparing the Akaike information criterion, corrected for a small sample size (AICc). Models were validated through standard protocols (examination of residuals, model fit, dispersion, autocorrelation), and the estimated mean and 95% confidence intervals calculated. For models containing an interaction, post-hoc planned comparisons of each predictor variable were performed (Appendix S3.2, S3.3). GLMMs were fitted using the glmer function in the lme4 package, and plotted with ggplot2, in R (Team RC 2016).

3.4 Results

3.4.1 Effects of typhoons, island type and NTMR protection on benthic composition and percent cover

Typhoons caused the clearest differentiation in benthic composition (Fig. 3.2a-b). Typhoon affected reefs were characterised by sand and rubble, or bedrock covered in EAM, while reefs not affected by typhoons had a range of living biota (Fig. 3.2g-h). Typhoons affected reef crests more severely than reef slopes (PERMANOVA, Appendix S3.2). In the absence of typhoons, there were distinct differences in the benthic composition between mainland and offshore islands (Fig. 3.2c-d). Mainland island reefs

were characterized by robust hard corals and macroalgae, while offshore islands were characterised by fragile hard corals and soft coral (Fig. 3.2g-h). Structure of coral reef benthos was not clearly nor consistently different between NTMRs and fished areas, irrespective of island type or typhoon impacts (Fig. 3.2e-f; PERMANOVA, Appendix S3.2).

Percent cover of both fragile and robust hard corals were best explained by typhoon impact, island type, and their interaction, but not NTMR status. There was significantly less cover of fragile corals (Fig. 3.3a-b, GLMM estimate [95% CI]: crest – 0.28 [0.11, 0.68] p=0.005, slope – 0.40 [0.21, 0.76] p=0.005) and robust corals (Fig. 3.3c-d, crest – 0.32 [0.19, 0.54] p<0.001, slope – 0.32 [0.2, 0.51] p<0.001) on typhoon-affected reefs at both island types (Appendix S3.3).

Macroalgal cover was best explained by island type, NTMR status, and their interaction, but not by typhoon impact. Macroalgal cover was always higher on mainland islands than offshore islands (Fig. 3.3e-f) and significantly so on reef slopes (Appendix S3.4). Macroalgal cover was always lower in NTMRs than in fished sites (GLMM, estimate [95% CI]: crest – 0.58 [0.40, 0.85] p=0.004, slope – 0.57 [0.37, 0.87] p=0.01), although the difference was significant for mainland islands only (Fig. 3.3e-f, Appendix S3.3).

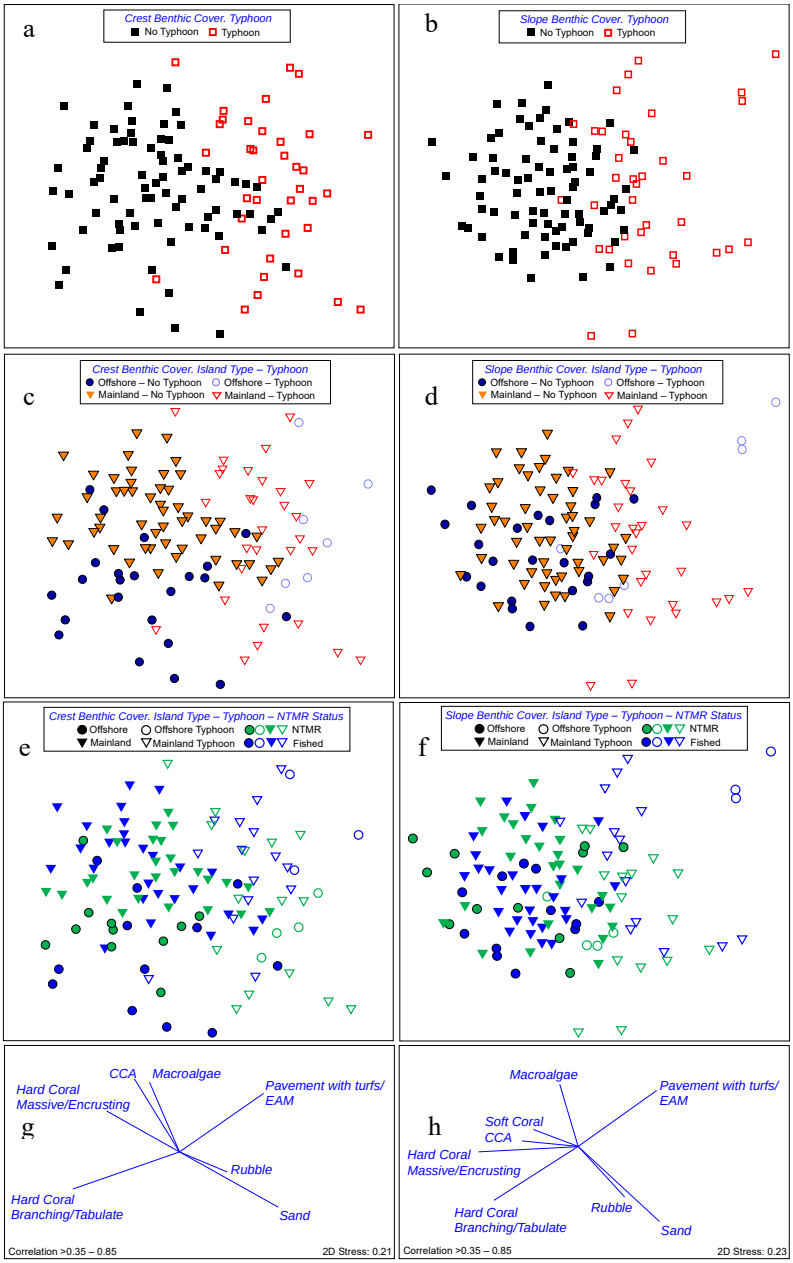

Figure 3.2. Non-metric multidimensional scaling analyses showing differences in benthic cover across factors of typhoon effect (a-b), the interaction between typhoon and island type (c-d), and the interaction between typhoon, island type and NTMR status (e-f), using transect level data for crests (left panels) and slopes (right panels). Vectors (g-h) represent partial regression coefficients of the original variables (benthic category percent cover) within 2 dimensions. Lengths of the vectors are proportional to degree of correlation. Significant differences in benthic assemblages were evident between typhoon (a – crest, pseudo-F=28.31, $p<0.001$; b – slope, pseudo-F=23.19, $p<0.001$), the interaction between typhoon and island types (c – crest, pseudo-F=3.76, $p<0.001$), d – slope, pseudo-F=4.78, $p<0.001$), and the interaction between typhoon, island types and NTMR status (e – crest, pseudo-F= 6.31, $p<0.001$; f – slope, pseudo-F=6.57, $p<0.001$). For pairwise comparisons of PERMANOVA see Table S3.3

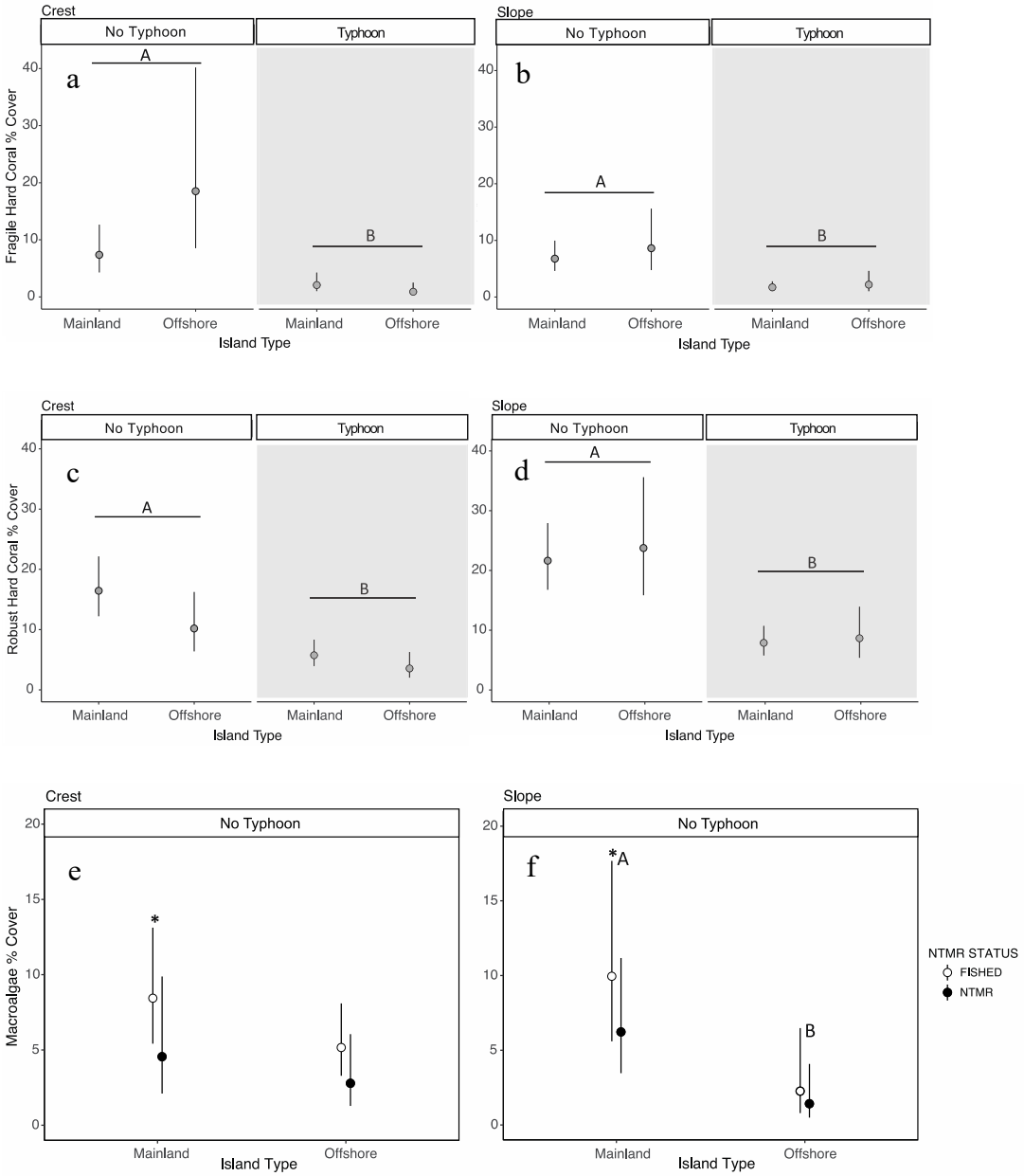

Figure 3.3. Estimates of the percent cover of benthic categories (y-axes) on reef crests (left panels) and slopes (right panels) for fragile hard corals (a-b), robust hard corals (c-d), and macroalgae (e-f) by island type (x-axes – mainland, offshore), typhoon effects (hard coral models only: unshaded facet – 'no typhoon', shaded facet – 'typhoon'), and NTMR status (macroalgal models only: filled points – NTMR, unfilled points – fished). Error bars are 95% confidence intervals. For fragile and robust hard coral cover, horizontal bars with unique letters indicate significant differences between typhoon damaged and undamaged sites, at both island types. For macroalgae, unique letters indicate significant differences between island types, and asterisks indicate significant differences between NTMR status and fished areas. As all models included an interaction, refer to Supplementary Material planned comparisons of each factor level.

3.4.2 Effects of typhoons, island type and NTMR protection on reef fish assemblages

Reef fish assemblage structure, based on density (the number of individual fishes per 1000 m^2), was most strongly affected by typhoons (Fig. 3.4a-b), then island type (Fig. 3.4c-d), then NTMR status (Fig. 3.4e-f). Typhoon-affected reefs had greater densities of rubble dwelling, small-bodied damselfish species and invertivorous wrasses than unaffected reefs (Fig. 3.4g-h). For island type, there was a significant difference in assemblage structure, measured as fish density, between mainland island reefs and offshore island reefs, regardless of typhoon affects (Fig. 3.4c-d). For reefs unaffected by typhoons, mainland island reef crests had higher densities of large-bodied benthic feeding surgeonfishes and wrasses, while offshore reef crests had higher densities of coral-associated damselfish (Fig. 3.4g). Offshore island reef slopes were characterized by large densities of planktonic-feeding fish species (Fig. 3.4h). Assemblage structure of reef fish based on density differed slightly but significantly between NTMRs and fished areas on offshore islands free of typhoon impacts (Fig. 3.4e-f; PERMANOVA, Appendix S3.2). These differences could not be attributed to any particular fish species (Fig. 3.4g-h).

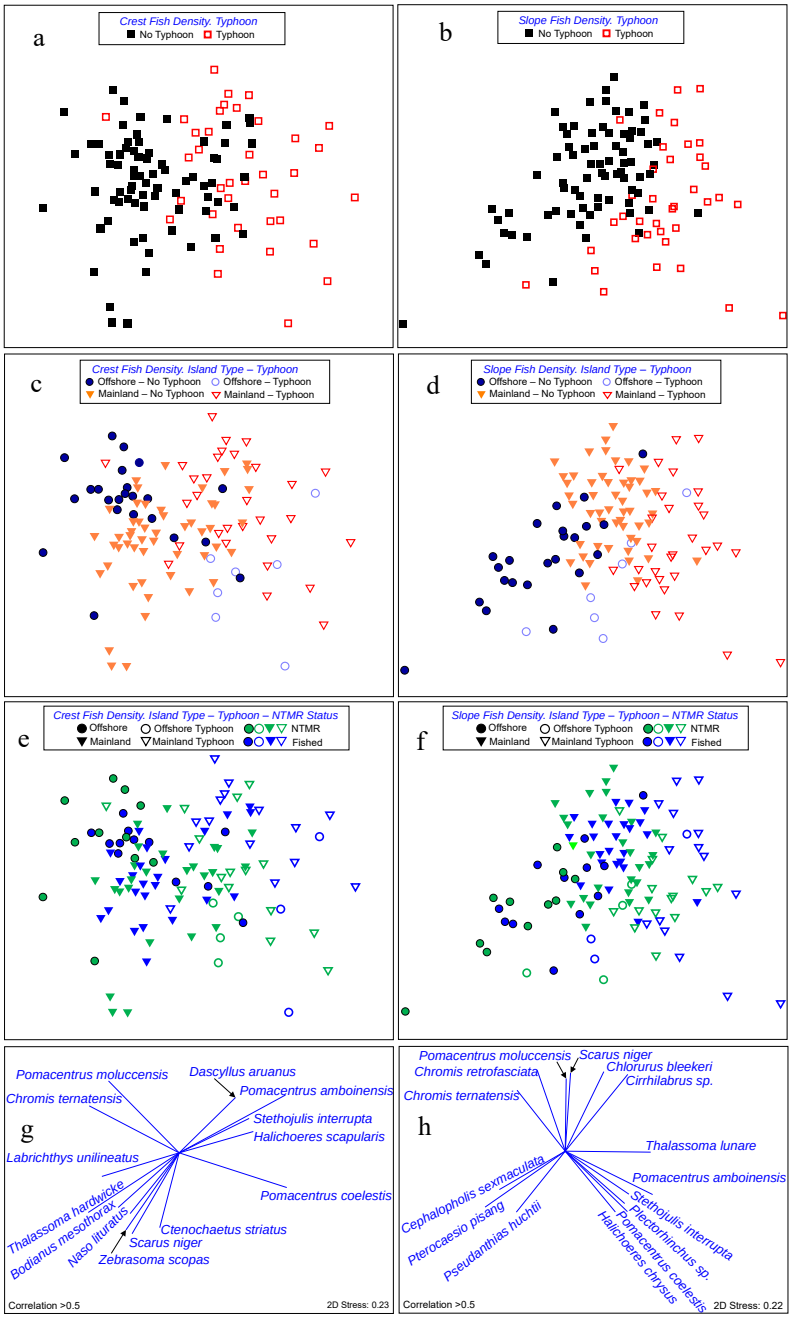

Figure 3.4. Non-metric multidimensional scaling analyses showing differences in density of all reef fish (abundance all fish species <10cm + >10cm TL per 1000m^2) across factors of typhoon (a-b), the interaction between typhoon and island type (c-d), and the interaction between typhoon, island type and NTMR status (e-f), using transect level data for crests (left panels) and slopes (right panels). Vectors (g-h) represent partial regression coefficients of the original variables (density of individuals within species) within 2 dimensions. Lengths of the vectors are proportional to degree of correlation. Significant differences in fish density were evident between typhoon effect (a – crest, pseudo-F=9.50, p<0.001; b – slope, pseudo-F=5.91, p<0.001), the interaction between typhoon and island types (c – crest, pseudo-F=3.77, p<0.001), d – slope, pseudo-F=2.99, p<0.001), and the interaction between typhoon, island types and NTMR status on reef crests (e – crest, pseudo-F=1.86 , p=0.02; f – slope, pseudo-F=1.41, p=0.112 NSD). For pairwise comparisons of PERMANOVA see Table S3.2.

The assemblage structure, based on biomass of large reef fish, differed clearly between typhoon effects (Fig. 3.5a-b) and island types (Fig. 3.5c-d), but only subtly with NTMR status (Fig. 3.5e-f). Reef fish assemblages offshore tended to retain their offshore characteristics, even when impacted by typhoons, more clearly for biomass than for density (Fig. 3.4c-d vs. 3.5c-d). Mainland island reefs had greater biomass of small-bodied parrotfish, and benthic feeding surgeonfish, regardless of typhoon damage (Fig. 3.5g-h). Biomass of offshore island reef crests was characterised by large-bodied parrotfishes (Fig. 3.5g), and offshore island slopes by planktivorous species (Fig. 3.5h). NTMRs had a significantly different assemblage structure of large fish biomass compared to fished areas on offshore islands free of typhoon impact, and on mainland islands that were typhoon-impacted. Under other conditions, NTMRs did not significantly affect the composition of species contributing to biomass (Appendix S3.2).

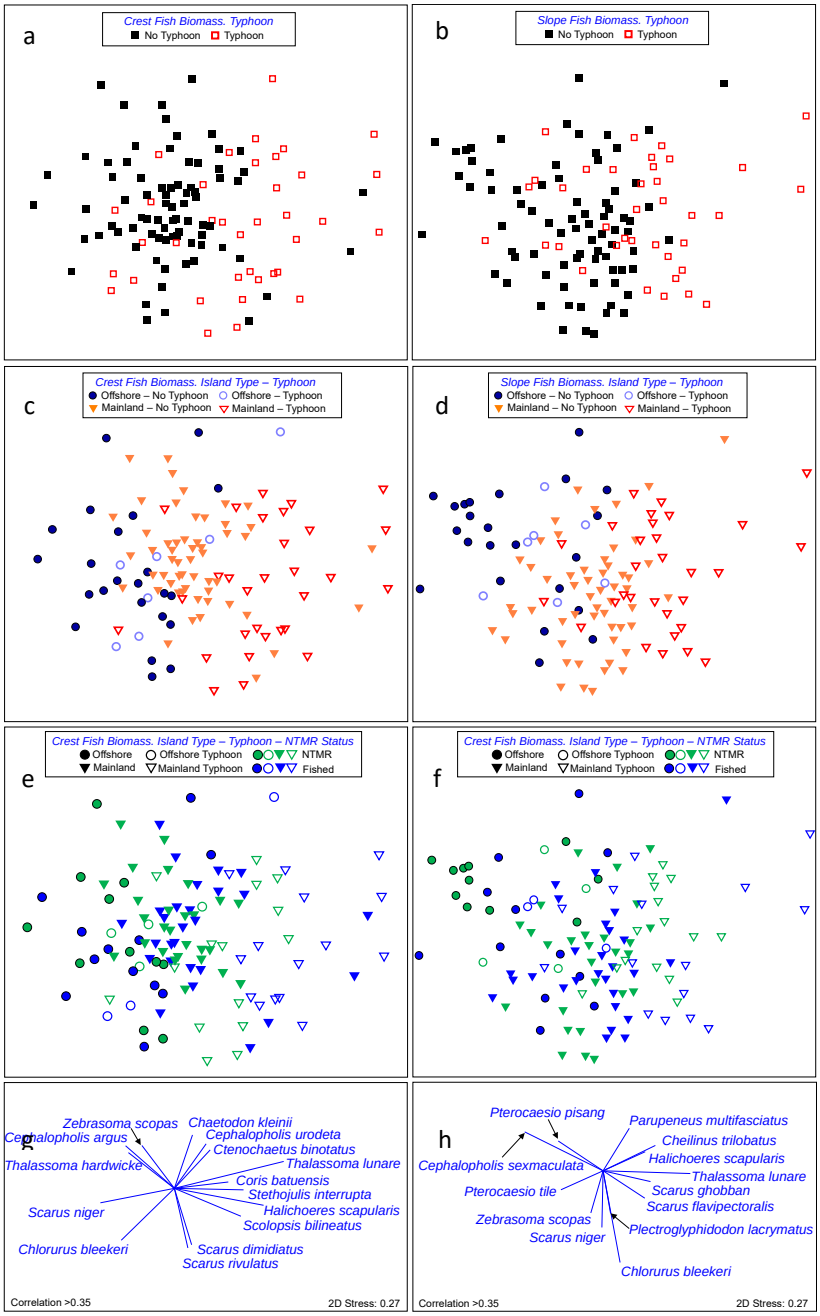

Figure 3.5. Non-metric multidimensional scaling analyses showing differences in biomass of large reef fish (kilograms of fish >10cm TL per 1000m^2) across factors of typhoon (a-b), the interaction between typhoon and island type (c-d), and the interaction between typhoon, island type and NTMR status (e-f), using transect level data for crests (left panels) and slopes (right panels). Vectors (g-h) represent partial regression coefficients of the original variables (biomass of individual species) within 2 dimensions. Lengths of the vectors are proportional to degree of correlation. Significant differences in fish biomass were evident between typhoon (a – crest, pseudo-F=4.75, p<0.001; b – slope, pseudo-F=3.16, p<0.001), the interaction between typhoon and island types (c – crest, pseudo-F=2.84, p<0.001, d – slope, pseudo-F=2.69, p<0.001), and the interaction between typhoon, island types and NTMR status on reef slopes only (e – crest, pseudo-F=1.56, p=0.052 NSD; f – slope, pseudo F=1.85, p=0.01). For pairwise comparisons of PERMANOVA see Table S.3.2

However, total biomass of reef fish (>10cm TL) was always higher in NTMRs than in fished areas (Fig. 3.6a-b, GLMM estimate [95% CI]: crest – 1.73 [1.42, 2.14] p<0.001, slope – 1.35 [1.03, 1.75] p=0.028), at both island types, whether typhoon affected or not. Offshore island reefs always had higher total biomass of large reef fish than mainland island reefs (Fig. 3.6a-b, crest – 1.99 [1.42, 4.13] p<0.001, slope – 3.25 [2.08, 5.10] p<0.001). Typhoon damaged reefs always had a lower total fish biomass than reefs not damaged (Fig 3.6a-b, crest – 0.56 [0.41, 0.76] p<0.001, slope – 0.49 [0.33, 0.73] p<0.001).

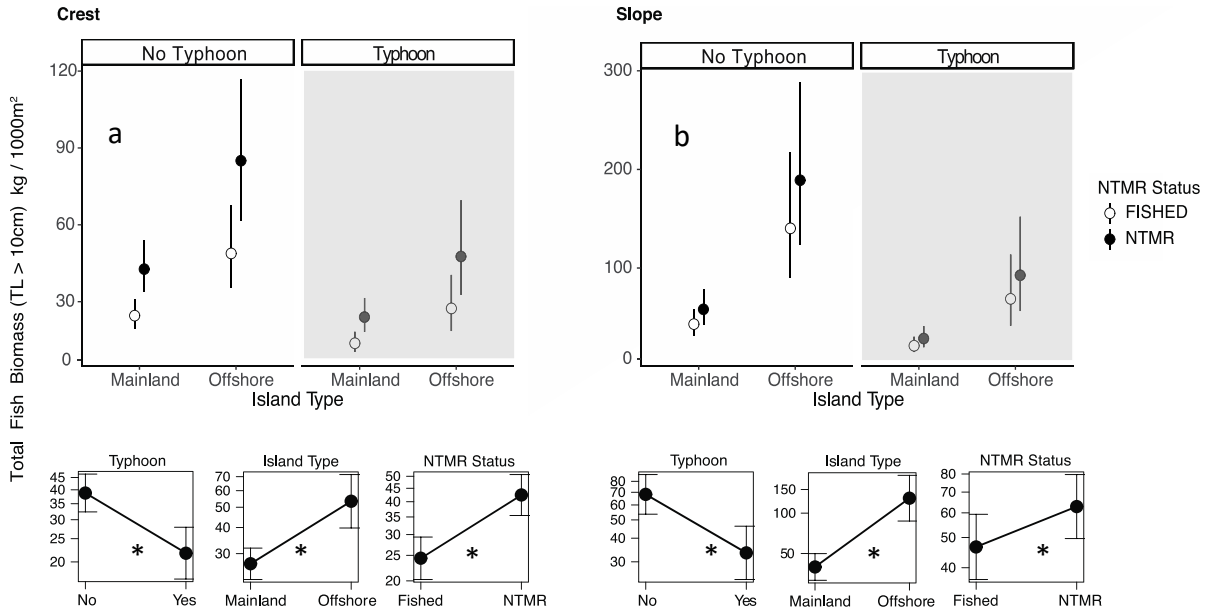

Figure 3.6. Estimates of large fish (> 10cm TL) biomass (a-b) (kilograms/1000 m^2) on reef crests (left panels) and slopes (right panels), by island type (x-axis – mainland, offshore), typhoon effects (inner facets: unshaded – 'no typhoon', shaded – 'typhoon'), and NTMR status (filled points – NTMR, unfilled points – fished). Top panels display modelled estimated mean biomass with 95% confidence intervals across factor levels. Bottom panels display factor effects of the best GLMM. Asterisks above data points indicate significant differences (p<0.05) between levels of each factor.

3.5 Discussion

3.5.1 Relative effects of typhoons, island type and NTMRs on coral reef benthic and fish assemblages

The assemblage structure of reef fish and the benthos was driven primarily by typhoon impact and island type, but not greatly influenced by NTMRs. However, the total biomass of large reef fish responded to typhoon impact, island type and NTMRs. Thus, NTMRs did not consistently affect the assemblage structure of species relative to fished places. But NTMRs did consistently have higher total biomass of large fish relative to fished areas, across all levels of island type and typhoon damage. There were subtle differences in fish assemblage structure between NTMRs and fished reefs on offshore islands free from typhoon damage (density and biomass), and mainland islands that were typhoon damaged (biomass only). NTMRs did not have an obvious or consistent effect on benthic composition nor total hard coral cover. But NTMRs did consistently have lower total macroalgal cover relative to fished areas, particularly on mainland islands.

3.5.2 Typhoon-NTMR effects on benthic and fish assemblages

Severe typhoon disturbance to the benthos appeared to have greater impacts on the assemblage structure of reef fish density than on the assemblage structure of reef fish biomass. This strong response of fish density to typhoon impacts is likely due to the dependency of small reef fish on fine-scale coral habitat for food and shelter (Jones et al. 2004, Pratchett et al. 2011). That reef fish biomass did not respond as strongly as density to change in benthic cover may reflect the ability of some large-bodied species to forage, persist, and even increase in density in areas of reduced structural complexity and live

hard coral cover, such as parrotfishes (Nash et al. 2016, Russ et al. 2015) and detritivorous surgeonfishes (Russ et al. 2018).

The finding that NTMRs impacted by typhoons still had higher fish biomass than fished areas impacted by typhoons is important for community-based fisheries management initiatives. In instances where NTMRs avoid major environmental disturbances by chance, NTMRs will likely play an important role as sources of recovery for the entire reef system (Williamson et al. 2014, Roberts et al. 2017). However, even if NTMRs and fished areas are damaged to the same extent by disturbance, the loss of fish biomass in NTMRs may be buffered simply because NTMRs should have more fish biomass to lose, and thus, more fish biomass to retain. Results of this study showed higher biomass of fish inside NTMRs relative to fished areas despite typhoon damage. Thus, even typhoon-damaged NTMRs may play a role in the recovery of fish assemblages, and importantly, in the supplementation of fisheries. Furthermore, as larval connectivity links offshore to mainland islands (Abesamis et al. 2017), NTMRs throughout the region may provide a source of breeding biomass of reef fish that resupply offshore and mainland NTMRs, and fished areas. However, not all reef fish species will persist in benthic habitats severely damaged by typhoons (Wilson et al. 2006, Pratchett et al. 2011). Whether species thought to be important for maintaining ecosystem processes will be among those that persist has not been tested here, and so continued monitoring of typhoon damaged reefs will be important in understanding reef recovery trajectories in the long term (McClure et al. 2019). Nevertheless, from the perspective of local fisheries management initiatives, higher fish biomass inside than outside NTMRs on typhoon damaged reefs is a positive and noteworthy finding.

3.5.3 Island Type-NTMR effects on benthic and fish assemblages

The marked differences in benthic composition, reef fish assemblage structure, and total biomass of large reef fish between island types likely reflects the different geomorphology and environmental conditions among and within island types, respectively (Wilkinson and Cheshire 1988, Fabricius 2005, Cheal et al. 2013, Taylor et al. 2015, Heenan et al. 2016). For example on offshore islands, wind direction, waves and currents affect local geomorphology and thus benthos. Meanwhile local upwelling may influence nutrient availability for plankton, in turn driving the abundance of small planktivorous reef fish, their predators (Wolanski and Hamner 1988, Duarte and Garcia, 2004), and larger-bodied schooling, reef-associated planktivorous species (Hamner et al. 1988, Khalil et al. 2017, Russ et al. 2017). Offshore reefs in this study had greater biomass of large reef fish than mainland reefs, especially in NTMRs.

Despite inherent differences of coral reef assemblages between mainland and offshore islands, both island types provide important sources of fisheries, biodiversity and connectivity (Almany et al. 2009, Abesamis et al. 2017), and so both are worthy of protection. While isolated offshore island reefs have more fish biomass than mainland reefs, they host a different assemblage of fishes and have a different suite of pressures. For example, fishing pressure on coastal reefs may be higher than on reefs further from large villages (Cinner et al. 2013), and so the need for coastal NTMRs is potentially more critical to support local protein needs of people (Huijbers et al. 2015). Furthermore, while NTMRs in coastal environments may have greater exposure to rivers and urban developments than offshore NTMRs, coastal NTMRs can be as successful for conservation and fisheries management (Huijbers et al. 2015). In addition to the ecological and fishery benefits of NTMRs, involvement of coastal human communities in

NTMR implementation and maintenance can increase understanding of conservation and resource management (Alcala and Russ 2006, Huijbers et al. 2015, Dalton 2005) and help to enhance compliance, one of the most essential components of NTMR success (Campbell et al. 2012, Bergseth et al. 2015).

NTMRs had slightly, but significantly, different assemblage structure of reef fish than fished areas on offshore islands free of typhoon damage (density and biomass), and on typhoon-damaged mainland islands (biomass only). That offshore NTMRs had a different fish assemblage structure than offshore fished areas in terms of both density and biomass might be attributed to two mechanisms. The intensity of fishing pressure in fished areas may be undermining the integrity of fish assemblages (Roberts 1995), and/or, NTMRs may have been placed (deliberately or by chance) in conditions not favourable to fishing, but favourable to high densities of all fish, and high biomass of large fish. Indeed, it is a common concern of conservation planning that NTMRs are placed where fishers would not choose to fish anyway (see Edgar et al. 2004). However, it is not possible to tease apart the relative contribution of fishing pressure and NTMR placement from current analyses.

The difference in assemblage structure of reef fish biomass between NTMRs and fished areas on typhoon-damaged mainland islands is attributable to a mechanism of fishing pressure interacting with degraded habitat. This NTMR effect did not hold for mainland islands with no typhoon damage, indicating that perhaps fishing does not substantially modify the assemblage structure of reef fish in the absence of other large-scale pressures, but the combination of fishing, coastal runoff, and extreme disturbance act in synergy to degrade assemblage structure (see Roberts 1995). Nearshore fish assemblages generally have lower diversity, and thus less redundancy, than offshore assemblages (Cheal et al.

2013), and these differences are even clearer after cyclones and coral bleaching (McClure et al. 2019). Thus, prioritizing damaged and environmentally stressed nearshore reefs for management action, including greater control of land-use practices to improve quality of water run-off onto reefs, should be beneficial.

3.5.4 NTMR-specific effects on benthic and fish assemblages

Total biomass of large fish was consistently higher in NTMRs than fished areas, across all conditions of island type and typhoon damage. This is surprising, as while most large fish species are retained by fishers, not all fish species that contribute to biomass are preferentially targeted. Yet, the multi-species, multi-trophic level nature of reef fisheries in the Philippines, the absence of restrictions on fish retention sizes, non-specific gear types (Alcala and Russ 2002) and relatively uniform targeting across most families of reef fish (Russ and Alcala 1998), coupled with a lack of evidence of an NTMR effect on benthos, suggests that the NTMR effect on fishes observed in this study was a result of protection from fishing. Another possible explanation could be a reef fish settlement bias towards NTMRs, however this is unlikely given the very small size of most NTMRs and the good connectivity and recruitment among fished areas and NTMRs (Abesamis et al. 2017).

NTMRs had little detectable effect on benthic assemblages, and no effect on the percent cover of live hard corals in this study. Thus, protection against fishing, or other destructive human practices, is not having a significant direct or indirect effect on live coral assemblages (Emslie et al. 2015, Russ et al. 2015b). Either, human activities directly destructive to benthos are not prevalent in areas open to fishing, and/or, protection of fish assemblages in NTMRs is not causing top-down control of the benthic

assemblage. The lack of consistent NTMR effect on benthic assemblages in this study is perhaps not surprising given that fishing and tourism practices in the Philippines have improved in recent decades. Destructive muroami drive-net fishing was banned in 1986, and similar less destructive modifications banned in 2000 (Butcher 2004). Nets and fish traps that can damage corals to moderate levels are used widely in the Philippines, including in the region of this study. However, surveys were not performed on the reef flat or back reefs where much of the net fisheries and anchoring of tourist boats occurs, nor on deep reef slopes where much of the trap fishing occurs. Thus, surveys may not have captured all potential NTMR effects. Where fishing practices destructive to benthos are present elsewhere in the tropical Pacific, NTMRs have caused a direct improvement of the benthos (Campbell et al. 2012). Yet neither direct (fishing practices affecting the benthos) nor indirect (protected fishes affecting the benthos) effects of NTMRs on coral cover were evident in this study.

In contrast, NTMRs did affect the cover of macroalgae. Macroalgal cover was lower in NTMRs than fished areas on both reef crests and slopes. This pattern was significant on mainland island reefs where nutrients from land-runoff are presumably higher than on the relatively isolated offshore island reefs where terrigenous inputs are low. A lower percent cover of macroalgae inside NTMRs is possibly a direct effect of protecting herbivorous fishes that either directly or indirectly influence algal cover (Stockwell et al. 2009). Direct effects of NTMRs on macroalgal cover can occur in locations with high levels of fishing pressure on fish species that directly consume macroalgae, particularly on coastal coral reefs where macroalgae is more prevalent (Rasher et al. 2013, Stockwell et al. 2009). Conversely, NTMR effects on macroalgal cover are less evident or absent where the herbivorous fish do not target macroalgae (Ledlie et al. 2007), when herbivorous fish are not targeted by fishers, as on the GBR (see Emslie et al. 2015, Casey

et al. 2016), or on relatively isolated coral reefs in clear offshore waters with naturally low macroalgal cover (Russ et al. 2015). Results from this study included a combination of all of these conditions, including a weak NTMR effect on macroalgae on offshore reefs, and a clear NTMR effect on macroalgae in relatively nutrient rich waters where herbivores, including urchins, are targeted.

3.6 Conclusions

No-take marine reserves remained successful in their primary goal as fisheries management tools, by having higher reef fish biomass relative to fished areas, irrespective of island type and typhoon disturbance. Typhoons caused substantial loss of live hard corals regardless of NTMR status, yet biomass of large reef fish was still higher in NTMRs than fished areas. This is encouraging for coral reef fish population recovery following environmental disturbances and particularly important for fisheries sustainability in a region highly dependent on coral reef fish for food security (Cabral and Geronimo 1998). Mainland island reefs had much less fish biomass and density than offshore island reefs, regardless of NTMR protection or typhoon damage. Whether this is due to natural spatial differences in environmental conditions, the likely higher terrestrial inputs onto reefs of mainland islands, or due to higher fishing pressure on mainland islands compared to offshore islands, cannot be determined from current analyses. Thus, determining factors that drive the structure of reef fish assemblages, particularly of those species that are regularly targeted by fishers, will assist in identifying the relative contribution of environmental and human factors to the success of NTMRs as fisheries management and conservation tools into the future.

Chapter 4:

Environmental factors have a greater effect on reef fish density and richness than fishing in the Philippines

4.1 Abstract

Whether assemblages of species respond more strongly to bottom-up (availability of trophic resources or habitats that provide such resources and shelter) or top-down (predation pressure) processes is a classic and continuing debate in ecology. Potentially, both of these processes can be important simultaneously. Thus, understanding their relative contributions is necessary for effective management of resources and ecosystems. Here, I utilise a multi-species fishery in a complex coral reef seascape in the Philippines to determine the relative influence of habitat-level, island-level, and fishing effects in driving the density and species richness of four coral reef fish groups targeted by fishing, and the density of two groups not targeted by fishing. Boosted regression trees were used to model the response of each fish group to 20 predictor variables that included no-take marine reserve (NTMR) presence-absence, size and age. Results showed that fish groups most strongly responded to habitat-level, then island-level characteristics. Of the habitat-level characteristics, live hard coral cover, structural complexity and depth accounted for the most influence on fish density and richness across all six fish groups. Distance from reef to river, and island elevation were the most influential island-level characteristics. NTMRs were influential only on fishes targeted by fishing, such as mesopredatory, grazing and detritivorous fishes, but the effects of NTMRs were small compared to habitat- and island-level effects. When influential, NTMR size positively correlated with density and species richness of targeted fishes, with NTMRs as small as 15 hectares producing positive effects. These results are important for developing island nations such

as the Philippines, which rely on small-scale community-managed NTMRs to support reef fisheries. Thus, integrated management strategies that incorporate sound coastal land use practices to protect fish habitat, with strategic placement of NTMRs, will be important in maintaining biodiversity and fisheries for the future, particularly in the region studied.

4.2 Introduction

Ecological drivers of population abundance, and the structure of species assemblages and ecosystems are believed to be either resource (bottom-up) or predation (top-down) dependent (McQueen et al. 1986, Leroux and Loreau 2015). While there are examples of both processes being prevalent in terrestrial (Gruner 2004, Elmhagen and Rushton 2007, see Hanley and Pierre 2015) and aquatic systems (Menge and Sutherland 1976, Shears and Babcock 2003, Smith et al. 2010, Boyce et al. 2015, Russ et al. 2015), the question of whether bottom-up or top-down processes drive ecosystem structure is of continued discussion in ecology. However, the complexity of forces that shape assemblages are likely scale- (local vs. regional) or context-dependent and influenced by the interaction of species with their environment (see Hunter and Price 1992, Shears et al. 2008, Leroux and Loreau 2015). Thus, understanding the relative influence of bottom-up and top-down processes in determining species assemblages is essential for designing successful management strategies for the conservation of natural resources and biodiversity.

On tropical coral reefs, the responses of coral reef fishes to changes in the benthos suggest a primacy of bottom-up processes in driving coral reef assemblages. For example, the majority of reef associated fish species rely on live hard coral for some part of their life history (Wilson et al. 2006, Coker et al. 2014). Increasingly well documented

is the decline in coral dependent fish species richness and density with the decline in live hard coral cover (Jones et al. 2004, Wilson et al. 2006, Emslie et al. 2015, Leahy et al. 2015), or the increase in dominance of coral reef associated species that benefit from loss of live coral and the associated increase in preferred feeding substrata following chronic or acute disturbance regimes (Wilson et al. 2006, Adam et al. 2011, Gilmour et al. 2013, Russ et al. 2015; 2018, McClure et al. 2019). Thus, live hard coral cover and reef structure are vital sources of food and shelter for fishes.

On the other hand, humans are the ultimate coral reef fish predators. On many tropical coral reefs, human overexploitation of fishes is recognised as a major contributor to the demise of coral reef species diversity, assemblage structure and overall resilience (e.g. Roberts 1995, Newton et al. 2007, Jackson et al. 2014). Yet fishing is just one threat identified to elicit such ecosystem responses, with multiple stressors of climate extremes, modified ocean chemistry, pollution, sedimentation and coastal development acting concurrently (Lubchenco et al. 2003, Hoegh-Guldberg et al. 2007) and importantly, destroying habitat resources for coral reef fishes (see Munday et al. 2008, Hoey et al. 2016). Nevertheless, as coral reef fish assemblages are undoubtedly modified by overfishing, supported by coral reef benthic habitat, and relied upon for ecosystem and human prosperity, identifying the relative influence of habitat (that provides trophic resources and shelter) and fishing in driving coral reef fish assemblages is important for improved coral reef management.

Coastal coral reefs in developing island nations are of particular management concern (Hoegh-Guldberg et al. 2010). Here, community-managed no-take marine reserves (NTMRs) provide a relatively simple and cost-effective means of managing local coral

reef resources by eliminating direct human extraction (see Roberts et al. 2017). The majority of community-managed NTMRs in developing nations protect small areas of reef (<0.5km^2) and are positioned near the villages that guard them (McClanahan et al. 2006, Weeks et al. 2010). This proximity is advantageous for monitoring and enforcement (McClanahan et al. 2006), and for compliance, which is key for NTMR success (Samoilys et al. 2007, Campbell et al. 2012, Bergseth et al. 2015, Edgar et al. 2014). But such proximity to land can also be detrimental, increasing exposure of protected coral reefs to undesirable land-based stresses caused by human occupation (See Jones et al. 2004, Halpern et al. 2013, Huijbers et al. 2015, Hamilton et al. 2017). Nevertheless, coastal NTMRs work in their primary goal as fisheries management and conservation tools (see Huijbers et al. 2015), leading to their prolific implementation in recent years (Weeks et al 2010, Horigue et al. 2012). Furthermore, the small spatial extent, but widespread utility, of community-managed NTMRs means they protect coral reefs subject to a variety of habitat and environmental conditions from fishing, providing the opportunity to test questions of ecological processes in the absence and presence of fishing.

Thus, I compare multiple exploited and NTMR protected coral reef areas under a variety of environmental conditions, to assess the relative influence of bottom-up (habitat as a resource that provides food and shelter) and top-down (human predation through fishing – see Pinnegar et al. 2000) processes on determining the density and species richness of coral reef fish assemblages. Specifically, I sought to 1. understand whether bottom-up (habitat) or top-down (fishing) processes are the primary driver of the density and species richness of four coral reef fish trophic groups targeted by fishing, and the density of two fish groups not targeted by fishing, 2. assess the utility of small spatial scale management

initiatives in achieving conservation and fisheries benefits. To achieve these objectives, I utilised a multi-species fishery with high levels of fish exploitation outside of no-take marine reserves.

4.3 Methods

4.3.1 Study sites

This study was conducted in the Central Visayas region of the Philippines, where coral reef fish assemblages are species rich, and most fish families are utilised in fisheries (Russ and Alcala 1998, Nañola et al. 2011). The Philippines has the highest number of NTMRs globally, now totalling 1800 (Horigue et al. 2012). I surveyed 17 representative coral reefs across seven islands that varied in geomorphology (Figure 4.1, Chapter 3 – Table S3.1), and sampled an NTMR and an adjacent fished area at each of these 17 coral reef sites.

4.3.2 Assessment of benthic and fish assemblages

At each site, I surveyed benthic habitat, and the abundance and size of all diurnally active coral reef associated fish species, inside and outside of NTMRs (as per Chapter 2). Briefly, coral reef benthic and fish surveys were performed along three or four 50-metre transects in each of two habitats (reef crest and reef slope) at each site, resulting in 228 transects across 17 sites. Benthic habitat was surveyed along each transect line using a point-intercept method, with categories of biotic and abiotic habitat features (Table 4.1) recorded directly under the transect line at 50cm intervals, resulting in 100 points per transect. Larger mobile fish (>10 cm total length (TL)) were counted within a 5 m wide belt, while swimming parallel to the contour of the reef and simultaneously laying the transect tape to minimize disturbance to the fish (following Hoey et al. 2011). Smaller,

site-attached reef fish species (≤10 cm TL), such as damselfishes, small-bodied wrasses, and juveniles of roving adults, were counted within a 2 m wide belt during a return swim along each transect. Fish species were categorized into groups based on diet, feeding behaviour, trophic ecology (Froese and Pauly 2018) (Table S4.1), and susceptibility to the fishery (targeted vs. non-targeted) (Russ and Alcala 1998). While underwater visual census may underestimate both the size and abundance of predatory fishes compared to baited video or sampling by angling (Willis et al. 2000), it is assumed that any such underestimation would be equal for both NTMRs and fished areas.

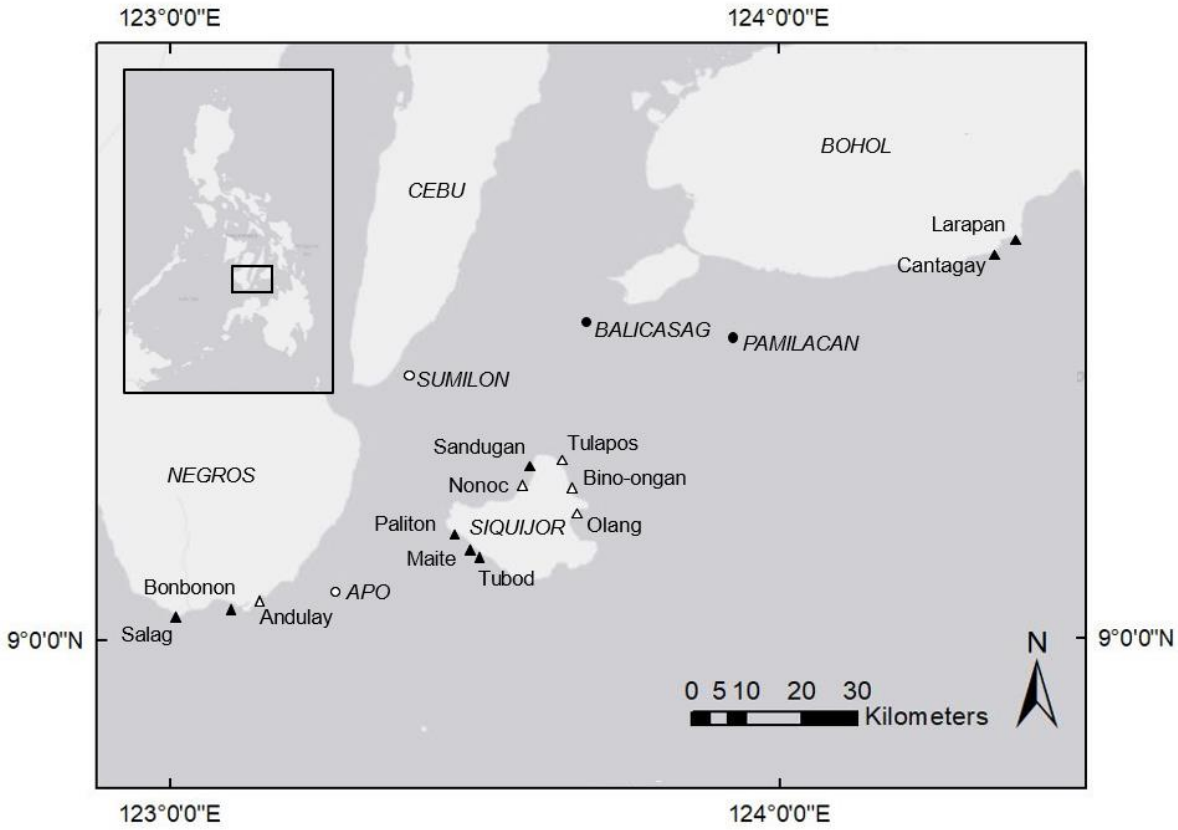

Figure 4.1. Map of the central Philippines showing the location of the 17 NTMR-fished pair sites, on mainland islands (triangles) and offshore islands (circles), including sites unaffected by typhoons (filled symbols) and those sites affected by typhoons (open symbols).

Table 4.1. Details of predictor variables used in BRTs

Predictor Category	Predictor	Abbrev.	Categorical or Continuous	Unit of Measure
Habitat-level environmental variables	Depth		Continuous	Meters
	Slope		Continuous	Scale 1 to 4
	Structural Complexity	StrC	Continuous	Scale 0 to 5
	Habitat Complexity Index	HCI	Continuous	Scale 1 to 50
	Fragile Hard Corals	HCBT	Continuous	% Cover
	Robust Hard Corals	HCME	Continuous	% Cover
	Epilithic Algal Matrix	EAM	Continuous	% Cover
	Macroalgae	MA	Continuous	% Cover
	Soft Coral	SC	Continuous	% Cover
	Rubble		Continuous	% Cover
	Zone		Categorical	Crest or Slope
	Typhoon Impact		Categorical	Yes or No
Island-level environmental variables	Distance to Nearest River		Continuous	Kilometres
	Distance to Shore		Continuous	Meters
	Island Elevation		Continuous	Meters
	Visibility		Continuous	Meters
	Island Type		Categorical	Mainland or Offshore
Fishing Effects	NTMR Protection Status		Categorical	NTMR or Fished
	NTMR Size		Continuous	Hectares
	NTMR Age		Continuous	Years
Other - Prey availability to mesopredators	Density of Fish ≤10cm TL		Continuous	Abundance (count)

4.3.3 Categorization of environmental variables, fishing effects and fish groups

For each site, additional environmental variables were recorded to capture multi-spatial scale characteristics that may influence the density and species richness of fishes (Table 4.1). All environmental variables were categorized as either a habitat-level characteristic, being indicative of the physical structure of the reef with which fish interact, or as an island-level characteristic, being indicative of broader environmental differences among and within islands (Table 4.1). The habitat-level parameters were benthic cover (hard coral (branching and tabulate, or massive and encrusting), soft coral, epilithic algal matrix

(EAM), macroalgae, rubble), structural complexity (following Wilson et al. 2007), reef slope, depth, reef zone, and typhoon impact. Habitat-level parameters were recorded at the transect level. A habitat complexity index (HCI) was also computed using estimates of live hard coral cover, structural complexity and slope (Abesamis and Russ 2005). The island-level parameters were island type, distance to shore, distance to nearest river, in-water visibility (measured along transect lines), and island elevation. Island-level parameters were estimated for each sampled NTMR and fished area and expressed as categorical or continuous variables (Table 4.1). Distance to shore and distance to nearest river were calculated using Google Earth as the average (from 5-points) linear distance in meters from the reef crest to the nearest shore, or river. Island elevation was calculated using Google Earth as the highest point of vertical elevation (m) within 2km of the shore adjacent to each site. Protection status of each transect was either open to fishing, or NTMR protected. NTMR size (hectares) and age (years) were recorded for NTMRs (Alcala et al. 2008). Fished areas were assigned a size and age of zero. Additional metrics of fishing pressure such as fishing effort were not available.

To assess the relative influence of habitat variables (bottom-up), and fishing pressure (top-down) in driving the density and species richness of coral reef fishes I selected six fish groups that represented a range of trophic groups and vulnerabilities to fishing. These included four large-bodied (>10cm TL) groups typically targeted by fishing; the mesopredators, planktivores, grazer/detritivores, and scrapers, and two smaller-bodied groups not typically targeted by fishing; invertivores (largely Labridae), and small fish ≤10cm TL including the juveniles of species potentially targeted by fishing (Table S4.1).

4.3.4 Data analysis

Boosted Regression Trees (BRTs) (Elith et al. 2008) were used to determine the relative influence of up to 20 predictor variables (Table 4.1) on the density and species richness of the six fish trophic groups, and the percent cover of 'fragile' (branching and tabulate corals) and 'robust' (massive and encrusting corals) live hard coral, and macroalgae, across 228 samples (transects). Response variables were modelled using Poisson or Gaussian family error distributions (Table 4.2). Predictor variables were checked against one another for collinearity using Pearsons correlation equations and plots. While BRTs have the advantage of handling some degree of correlation of predictor variables, highly correlated (≥60%) or confounded variables should be removed to avoid false positive influence of one of the variables (Zuur et al. 2007). Here, this included using NTMR size and NTMR age in the same model (correlated), and using habitat complexity index (HCI) vs. individual variables of structural complexity, total coral cover and reef slope upon which HCI is calculated (and are thus confounded). As the influence of these variables on fish density and species richness were of particular interest, multiple candidate BRTs were run with each alternative variable. BRTs were run separately for each response variable (fish trophic group density/richness, or benthic group cover) with all non-correlated predictor variables included in the initial model run. Uninfluential predictors were sequentially eliminated with each subsequent run. A random number was included periodically as a predictor variable to determine the likelihood of predictor influence compared to random chance. The random number was regenerated between each run of the reduced BRT, and then removed from the last model run to obtain final metrics (Table 2). The 'best' model was determined by comparing the percent deviance explained by all candidate models ((mean total deviance – estimated cross validation deviance) / mean total deviance). Models that explained ≤25% deviance were not considered, which

included models for the species richness of non-target fish groups. BRTs were run in R using the *dismo* package with the gbm.step function (Elith et al. 2008). BRT Step encompasses automated cross-validation and tree optimization protocols. Model parameters were designed to optimize ecological relevance (tree complexity 3, learning rate 0.01-0.001, bag fraction 0.75, maximum trees 10,000).

Table 4.2. Parameters of final BRT models for each response variable

Response Metric	Response	Distribution Family	Learning Rate	Tree Complexity	Bag Fraction	Optimal No. Trees	Final No. Variables	% Deviance Explained
Benthic cover	Robust hard corals	Gaussian	0.01	3	0.75	800	4	51.3
	Fragile hard corals	Gaussian	0.01	3	0.75	4050	4	57.0
	Macroalgae	Poisson	0.001	3	0.75	5700	4	39.3
Fish density /250m^2	Targeted mesopredators	Poisson	0.001	3	0.75	4250	5	28.2
	Targeted grazers/detritivores	Poisson	0.005	3	0.75	6550	7	52.7
	Targeted large-bodied planktivores	Poisson	0.005	3	0.75	9250	5	47.5
	Targeted scrapers	Poisson	0.001	3	0.75	5200	7	29.0
	Non-targeted small fish (<10cm TL)	Poisson	0.001	3	0.75	1050	4	41.5
	Non-targeted invertivorous fish	Poisson	0.01	3	0.75	2200	5	39.0
Fish species richness	Targeted mesopredators	Poisson	0.001	3	0.75	650	4	38.0
	Targeted grazers/detritivores	Gaussian	0.001	3	0.75	8450	7	45.5
	Targeted large-bodied planktivores	Poisson	0.001	3	0.75	4350	5	32.5
	Targeted scrapers	Gaussian	0.001	3	0.75	4550	5	28.6

4.4 Results

4.4.1 The relative influence of habitat-level, island-level and NTMR variables on benthic cover

A combination of habitat- and island-level characteristics had the greatest influence on the cover of the three benthic variables. Fragile and robust hard coral cover were best explained by island-level characteristics of distance to shore and distance to river, habitat level-characteristics of depth and typhoon impacts, but not NTMR status, size or age (Fig. 4.2a, b, Table 4.3). Fragile hard corals were most prevalent at shallow reef depths free of typhoon impacts, when reef crests were a moderate distance from shore, and on reefs far from rivers (Fig. 4.2a). Robust hard corals were most prevalent as depth increased, in areas free of typhoon impacts, close to rivers, and were more strongly associated with high elevation islands. Macroalgal cover was explained primarily by island characteristics and habitat variables (Fig. 4.2c, Table 4.3). Macroalgal cover was prevalent on reefs where the reef crest was 250-500 m from shore, in close proximity to rivers, when the EAM and fragile hard coral cover was low (Fig. 4.2c). NTMR effects were not a significant predictor of macroalgal cover.

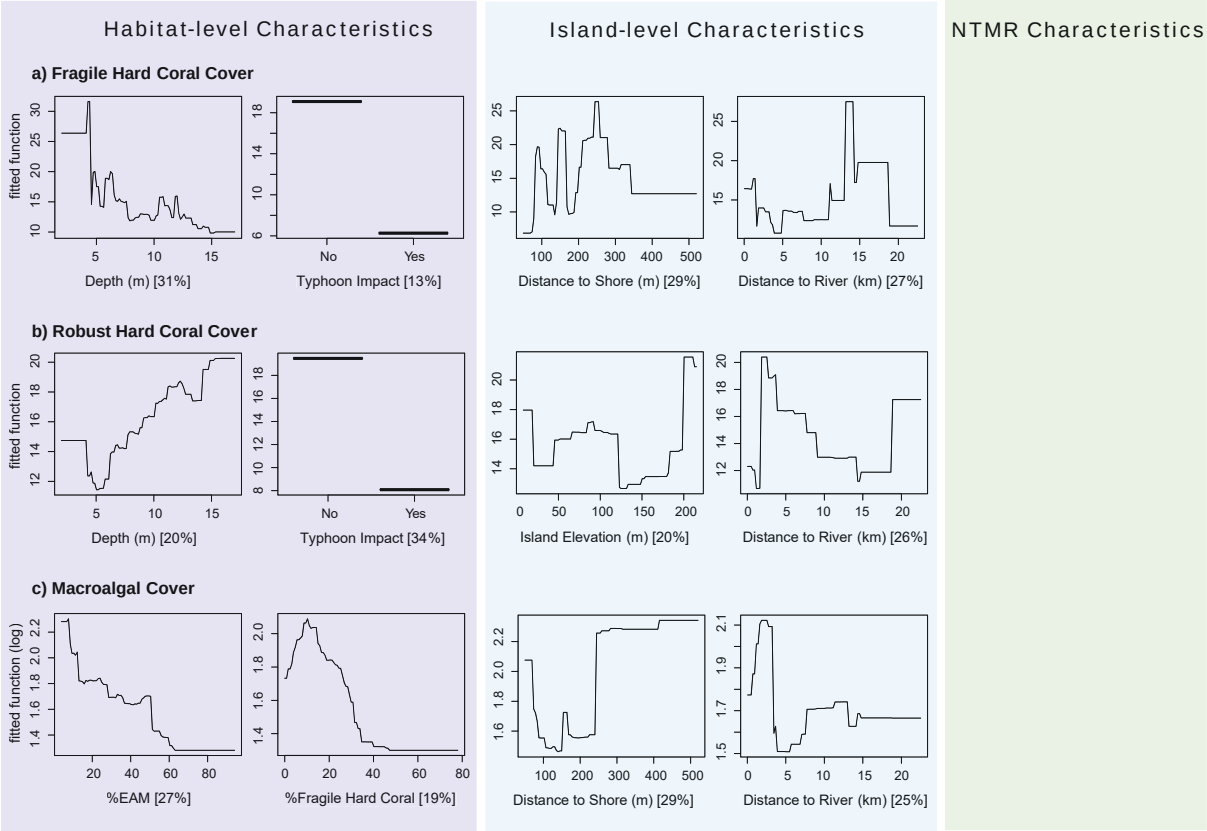

Figure 4.2. Partial dependence plots for all variables influencing the cover of fragile hard coral cover (a), robust hard coral cover (b), and macroalgal cover (c) in the final boosted regression tree models.

Table 4.3. Relative influence (%) of predictor variables for final BRT models of each response variable. Totalled relative influence of habitat-level and island-level categories are in bold.

Response		Habitat-Level Effects												Island-Level Effects						NTMR Effects			Other
		Depth	Slope	StrC	HCI	HCBT	HCME	EAM	MA	SC	Rubble	Zone	Typhoon Impact	**TOTAL HABIATT-LEVEL**	Distance to River	Distance to Shore	Island Elevation	Visibility	Island Type	**TOTAL ISLAND-LEVEL**	NTMR Status	NTMR Size	NTMR Age	Density Fish ≤10cm
Benthic cover	Fragile hard coral	31											13	**44**	27	29				**56**				
	Robust hard coral	20											34	**54**	26		20			**46**				
	Macroalgal cover					19		27						**46**	25	29				**54**				
Fish density /250m^2	Targeted mesopredators		7			45								**52**			10			**10**		7		31
	Targeted grazers/detritivores	22				12	11		9					**54**	24		9			**33**		13		
	Targeted large-bodied planktivores		9	15			40							**64**			27			**27**		9		
	Targeted scrapers			14			17			12				**43**	24		11	15		**50**			7	
	Non-targeted invertivores	22					37		14					**73**		18	9			**27**				
	Non-targeted fish ≤10cm TL	10			45			16						**71**			29			**29**				
Fish species richness	Targeted mesopredators				38									**38**			36			**36**		10		16
	Targeted grazers/detritivores	19				15			9					**43**	14	13	11			**39**		19		
	Targeted large-bodied planktivores	8	38			26								**72**	14	14				**28**				
	Targeted scrapers			16			22	14						**52**	34			14		**48**				

4.4.2 The relative influence of habitat-level, island-level and NTMR variables on density and species richness of fish trophic groups

The density and species richness of all targeted fish groups was primarily influenced by habitat-level parameters, then island-level parameters (with the exception of scraper density, where this pattern was reversed) (Fig. 4.3a-d, Fig. 4.4, Table 4.3). NTMR effects, when detected, were much less influential than the effects of habitat- and island-level parameters. The density of non-target fish groups was primarily influenced by habitat-level parameters, then island-level parameters, but was not influenced by NTMR status, size or age (Fig. 4.3e-f, Table 4.3).

Targeted mesopredator density (Fig. 4.3a) and species richness (Fig. 4.4a) were most influenced by the prevalence of habitat (density – fragile hard coral [45% relative influence]; richness – habitat complexity [38% relative influence]). Mesopredator density and species richness were higher on low elevation (offshore) islands than high elevation (mainland) islands, when the density of potential prey (fish ≤10cm TL) was high, and with increasing NTMR size [7, 10% relative influence density, richness respectively]. Targeted grazer/detritivore density (Fig. 4.3b) was most influenced by reef distance to rivers, and depth. Grazer/detritivore species richness (Fig. 4.4b) was most influenced by reef depth and NTMRs. Both density and species richness increased close to rivers, on shallow reefs, with increasing NTMR size, at moderate cover of fragile hard corals, high cover of robust hard corals (density only), and with increasing cover of macroalgae (Table 4.3). NTMRs had the most influence on grazer/detritivore density and species richness than on any other fish group, being the third (of seven) most positively influential variables for density and the equal first (of seven) most influential variable for species richness.

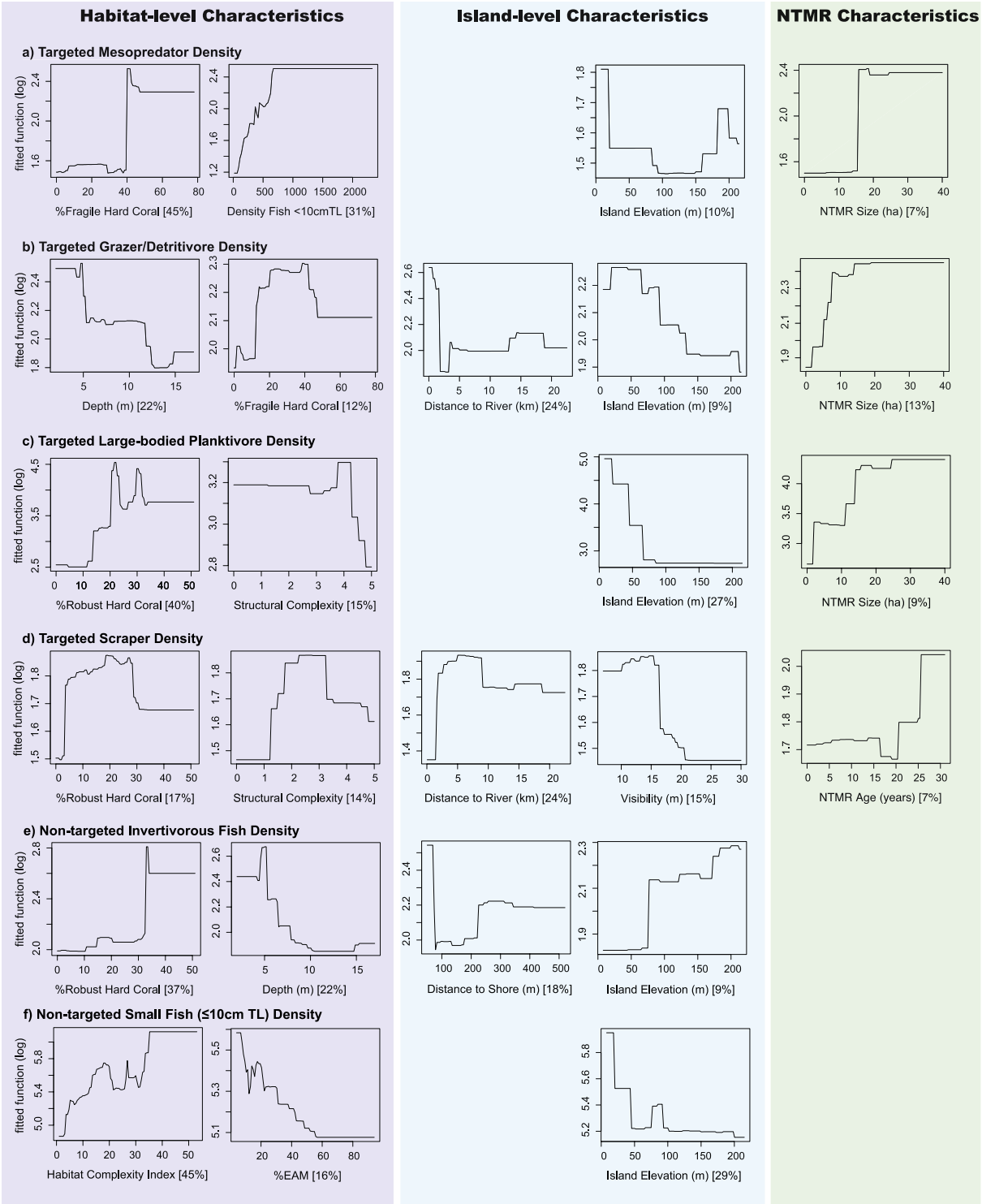

Figure 4.3. Partial dependence plots for variables influencing the density of targeted fish groups (a-d) and non-targeted fish groups (e-d). The top two most influential variables from the categories of habitat-level and island-level characteristics, and the most influential variable of NTMR characteristics in the final boosted regression tree models are shown. The percent relative influence of each variable is listed in square brackets beneath each partial plot [%]. For relative influence of all variables see Table 4.3.

Targeted large-bodied planktivorous fish density (Fig. 4.3c) and species richness (Fig. 4.4c) was most influenced by habitat (density – robust hard coral cover [40%]; species richness – reef slope [38%]). Density and species richness of large-bodied planktivorous fish were highest on reefs with high coral cover, high structural complexity and steep reef slopes, on reefs associated with low elevation (offshore) islands (density only), and further from rivers (species richness only) (Table 4.3). NTMR size positively influenced the density (9% relative influence) but not the species richness of large-bodied planktivorous fishes.

Targeted scraper density (Fig. 4.3d) and species richness (Fig. 4.4d) were highest on reefs close to rivers, with low to moderate robust hard coral cover, when in-water visibility was lower than 15 m, and at moderate levels of structural complexity, soft coral cover (density only) and EAM cover (species richness only) (Table 4.3). NTMR age slightly, but positively, influenced the density (7% relative influence), but not the species richness of scrapers. However, as the largest increase in density with NTMR age occurred in the oldest NTMRs (on offshore islands), this response may be an island-level influence, and not necessarily an influence of long-term protection from fishing.

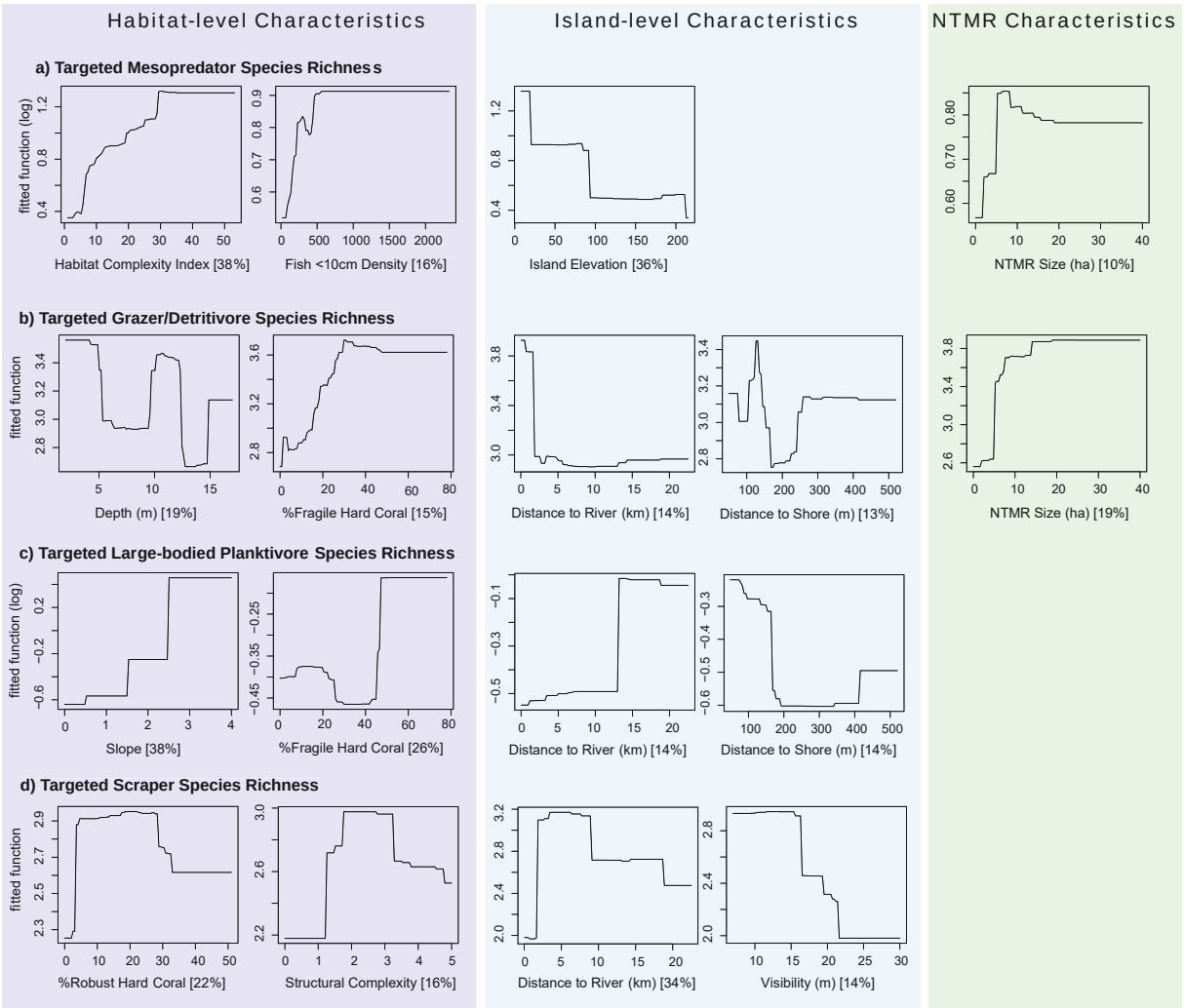

Figure 4.4. Partial dependence plots for variables influencing targeted fish species richness. The top two most influential variables from the categories of habitat-level and island-level characteristics, and the most influential variable of NTMR characteristics in the final boosted regression tree models are shown. The percent relative influence of each variable is listed in square brackets beneath each partial plot [%]. For relative influence of all variables see Table 4.3.

4.5 Discussion

Whether trophic resources and shelter (bottom-up processes), or predation (top-down processes) drive natural populations and assemblages remains a topic of continued discussion in ecology. Using a broader definition of bottom-up to include availability of trophic resources (including habitats that provide such resources) and shelter, this study

provides multiple lines of evidence that bottom-up processes are the primary driver of coral reef fish and benthic assemblages for the region studied. Top-down forces, observed when using NTMR protection as an unfished control, were weakly influential for density and species richness of fish groups directly targeted by fishing, such as herbivorous grazers and detritivores, and mesopredators. When influential, NTMRs as small as 15 hectares in size increased fish density relative to fished areas, demonstrating the importance of small NTMRs in community-managed initiatives in developing island nations.

That the density and species richness of coral reef fishes were principally influenced by bottom-up processes, irrespective of fishing pressure, is important for the development of conservation and resource management strategies, particularly in developing island nations that rely heavily on coral reef resources (Hoegh-Guldberg et al. 2010). Such coral reefs are often threatened by poor land-use management which adversely affects fish assemblages (Jones et al. 2004, Halpern et al. 2013, Hamilton et al. 2017), and by severe tropical storms and thermal bleaching which negatively affects coral reef fish habitats (Munday et al. 2008, Hoey et al. 2016). Thus, the incorporation of integrated coastal management strategies that prioritise mitigating run-off of sediments onto adjacent coral reefs (see Done and Reichelt 1998, Alvarez-Romero et al. 2011), and/or tactically placing NTMRs in regions less exposed to run-off and typhoons, as part of NTMR networks (see Hamilton et al. 2010), will likely assist in conserving important habitat for fishes. Environmental management strategies used in combination with simple, cost-effective fisheries management strategies of NTMRs will provide increased insurance for fisheries on a local scale.

Top-down effects of fishing, while less influential than habitat, negatively affected the density of all large-bodied fishes investigated, reinforcing the multi-species nature of Philippines fisheries (Russ and Alcala 1998). However, NTMRs were particularly important for determining not only the density, but species richness of grazing and detritivorous fishes (largely surgeonfishes, Acanthuridae), indicating that these groups are particularly affected by fishing. Indeed, life history traits of surgeonfishes (Choat and Axe 1996) makes these groups vulnerable to overfishing (Comeros-Raynal et al. 2012), though typically less so than mesopredatory fishes (see Abesamis et al. 2014). However, surgeonfishes are typically long-lived, slow to reproduce and thus slow to recover from exploitation (see Abesamis et al. 2014), and nominally herbivorous fishes that dominate reef flats and crests readily accessible to fishers are expected to become a major component of fisheries of the future, particularly in developing island nations (Taylor et al. 2014, Bellwood et al. 2018). Furthermore, evidence suggests that herbivorous fishes protected in coastal NTMRs provide benefits to the benthos through macroalgal reduction (Stockwell et al. 2009, Chapter 2). Thus, this study's findings of higher densities of herbivorous grazing and detritivorous fishes in proximity to rivers and human populations on mainland islands, combined with the high relative influence of NTMR protection on both species richness and density, shows that these fishes are a group of conservation importance in the Philippines.

Despite their small size, NTMRs still had a higher abundance of fishes susceptible to fishing than adjacent fished areas. This is a valuable finding for small-scale community-managed initiatives that are typical of resource management capabilities in developing island nations. Positive responses in fish density and species richness occurred in NTMRs as small as 15 hectares ($0.15km^2$), reinforcing that NTMRs need not be large to offer multi-species protection (see Lester et al. 2009), and subsidise fisheries (Abesamis

and Russ 2005, Samoilys et al. 2007). In contrast to these findings, some studies stress the importance of reserves being very large (10's of kilometres long) to achieve conservation and management goals (Edgar et al. 2014, Krueck et al. 2017). But community-based management initiatives rarely have the luxury of implementing NTMRs of this size. For the vast majority of stakeholders in developing nations these large reserves would displace too many fishers and will be the exception rather than the rule (Roberts et al. 2017). However, a concern of small reserves like those typical of the Philippines is that the home range of target species will exceed the area of protection (see Green et al. 2015). Nevertheless, the benefit of small community-managed NTMRs can be enhanced through connectivity among NTMRs and fished areas through fish larval dispersal, such that they form NTMR networks (Almany et al. 2013, Green et al. 2015, Abesamis et al. 2017). Thus, many well-managed, small, connected NTMRs with sound compliance might provide as much community benefit as large reserves with potentially unpatrollable boundaries.

This study has shown that the relative influence of drivers of fish assemblages are dominated by habitat-level characteristics, followed by island-level characteristics, then NTMR effects. The clear positive relationship of the density of all fish groups with increasing hard coral cover, structural complexity, and depth, irrespective of NTMR protection, reinforce bottom-up influences of habitat as the primary driver of reef fish assemblages (Jones et al. 2004, Russ et al. 2015, Emslie et al. 2015). This remained true even for groups that are highly targeted by fishing. For example, results showed that the density of mesopredators responded primarily to live hard coral cover, then to the density of highly habitat-dependent small (prey) fishes, indicating that habitat serves multiple roles as a resource. Coral reef fishes that are obligate feeders on live hard corals, such as butterflyfishes, have similarly been shown to be driven by changes in the benthos, but not

directly influenced by marine reserve protection (Jones et al. 2004, Leahy et al. 2015). Island-level influences (e.g. island elevation, distance to rivers) were particularly important drivers of the species richness of fish groups. Indeed, such spatial drivers are increasingly recognised as being important determinants of fish assemblage structure across broader spatial scales (Taylor et al. 2015, Heenan et al. 2016, Chapter 2), compared to fishing effects that tend to act locally on assemblage structure (Taylor et al. 2015). Nevertheless, NTMRs remained an important, but weaker driver for large-bodied fishes targeted by fishing. This may be particularly relevant for maintaining the density of targeted fishery species when habitat is adversely affected by localised stressors that are destructive to habitat (Emslie et al. 2015, Chapter 2). Thus, top-down and bottom-up processes in coral reef systems are likely not mutually exclusive (Shears et al. 2008, Leroux and Loreau 2015, Russ et al. 2015), and the relative influence of each process may be modulated by local and global stressors. Management strategies that prioritise maintenance of hard coral habitat for reef fishes, by incorporating improved coastal land use practices adjacent to coral reefs, together with the strategic placement of no-take marine reserves will help ensure fisheries for the future.

Chapter 5:

Using environmental indicators to investigate dietary plasticity in important coral reef fisheries species inhabiting different environmental conditions

5.1 Abstract

With increasing anthropogenic modifications to coral reef habitats and fish assemblages throughout tropical seas, understanding how ecologically and economically important fish species persist is a question of significance. Extremes in environmental conditions, such as excessive coastal runoff of sediments and nutrients, may modify the quality of food resources available to fishes, potentially influencing their persistence unless they can change primary dietary sources. This study uses stable isotope analysis to investigate the potential dietary plasticity of three common coral reef fish species across six coral reef sites of varying water quality in the central Philippines. Sedimentation rates, ^{15}N enrichment in the seaweed *Sargassum*, and turf algal productivity were measured to investigate if nutrient levels and algal resource availability differed among sites. Sedimentation rates varied three-fold among sites, greatest on reefs close to a large resort, and lowest on reefs farther from shore. Sedimentation rate was positively correlated to *Sargassum* $\delta^{15}N$ data, indicating different nutrient availability among sites. Sedimentation was negatively related to the growth of turf algal biomass. Given the evidence for environmental differences among sites, dietary plasticity in three large-bodied fishes that are known or suspected to consume benthic algae was investigated, by using stable isotope mixing models to link potential primary food sources to the body tissues of individual fish. Fish species were a macroalgal browser *Naso unicornis*, an algal cropper *Siganus virgatus* and a nominally planktivorous fish *Naso minor*. Potential primary food sources were plankton, *Sargassum*, turf algae, and detritus. Despite the

apparent differences in sedimentation, *Sargassum* ^{15}N enrichment, and turf algal productivity among sites, the relative importance of different dietary sources did not differ among sites within a species. However, the stable isotope mixing models suggest the three fish species were feeding on unexpectedly large proportions of some dietary sources. Isotopic signatures of fish consumers indicate that the nominally herbivorous species, *Siganus virgatus* was consuming moderate proportions of plankton, while the planktivorous species, *Naso minor* was consuming significant proportions of benthic algae. Thus, while there was limited evidence for dietary plasticity in *Siganus virgatus*, *Naso unicornis* or *Naso minor*, this study highlights these species ability to utilise local conditions.

5.2 Introduction

Coral reefs and their inhabitants experience a range of natural localized environmental conditions throughout their tropical distribution. However, natural fluctuations in prevailing conditions are increasingly exacerbated by poor land management practices, overpopulation and extreme climatic variation (Fabricius 2005, Munday et al. 2008, Hoegh-Guldberg et al. 2010). Land clearing for development and agriculture enhances inputs of terrigenous sediments and nutrients into coastal habitats (Hodgson and Dixon 1988, Smith et al. 1999, Davis et al. 2017, Hamilton et al. 2017). Similarly, rapid human population and tourism growth can lead to marine eutrophication when the appropriate infrastructure to support such human capacity, including basic sanitation and waste disposal, struggles to keep pace (e.g. See Lamb et al. 2017, Wong et al. 2019). Flood plumes onto coastal coral reefs following severe weather events can modify benthic resources available to fishes (Williamson et al. 2014, Olds et al. 2014, Hempson et al. 2017). Such events are expected to increase in severity with climate change, especially in

some of the world's poorest places that rely on coral reef fishes as sources of food and income (Hoegh-Guldberg et al. 2010, Mei and Xie 2016).

The capacity for fishes to adapt to a changing environment is variable, and likely attributed to their degree of habitat or dietary specialisation (Wilson et al. 2008, Hoey et al. 2016). For example, extreme changes such as loss of live coral cover from disturbance overwhelmingly lead to loss of fish species richness (but see Bellwood et al. 2006), particularly for coral dependent species (Jones et al. 2004, Pratchett et al. 2011, Coker et al. 2014). In these instances, some fish species may have the capacity to move location, or change their primary prey source (i.e. dietary plasticity), particularly larger-bodied predatory generalists (O'Farrell et al. 2014, Hempson et al. 2017, but see Feary et al. 2018 for dietary plasticity in a coral specialist). Less well known however is whether differences in environmental conditions across gradients of water quality (terrigenous input of sediment and nutrients) might modify resources available to fishes such that they need to change their primary food sources (exhibit dietary plasticity). As fishes abilities to adapt to environmental changes likely influences their persistence (Feary et al. 2018), this in turn may have consequences for ecological processes, and the success of fisheries that depend upon them.

Fisheries in developing nations rely on populations of fishes from multiple trophic levels. A great need for protein, coupled with diminishing availability of large-bodied predatory fishes, means that consumers of primary and secondary productivity (such as herbivores and planktivores) become exploited (Pauly et al. 1998). Fishing herbivorous and planktivorous species is believed to be detrimental for the maintenance of regular coral reef ecosystem services (see Pauly et al. 1998, Comoros-Raynal et al. 2012). For

example, herbivorous fishes can help regulate the biomass of algae on coral reefs through their feeding, when conditions favour algal productivity (McCook 1999, Russ 2003, Bauman et al. 2017). Planktivorous species provide food for higher order predators and constitute much of the biomass of coral reef fish assemblages (Hamner et al. 1988, Kingsford 1989, Khalil et al. 2017). Furthermore, some nominally planktivorous species (e.g. *Naso* spp.) may also incorporate macroalgae into their diets, as juveniles (Green and Bellwood 2009) or adults (Randall et al. 1986). However, fishing is rarely the only, nor the most pervasive threat, to fishes and their habitats (see Munday et al. 2008), even in developing nations. Excessive coastal runoff of sediments and nutrients can have consequences on resources of food and shelter available to fishes (Koop et al. 2001, Fabricius 2005, Tebbetts et al. 2018). For example, altered nutrient regimes can modify the availability or quality of resources for fishes (see Munday et al. 2008, Brierley and Kingsford 2009, Johnson and Welch 2009), putting into question the success of fishes for reefs and fisheries (Johnson and Welch 2009). It is therefore important to understand how fish that are integral to reefs and fisheries provision resources across differential inputs of terrestrially derived sediment and nutrient.

Stable isotopes of carbon and nitrogen have long been used in the study of animal diets and trophic position, respectively (Post 2002, Fry 2006). Increasingly, stable isotopes are being used in innovative ways to trace elements through marine systems. For example, the enrichment of elemental and isotopic nitrogen (^{15}N) in the leafy tissue of the seaweed *Sargassum* has been used as a proxy of relative nutrient availability among locations (Alquezar et al. 2013, Graham et al. 2015). Indeed, analysis of elements and their isotopes may be favourable over traditional analysis of water quality which is limited to indicating availability of in-water nutrients at a specific point in time, and does not

indicate what elements have been assimilated into living organisms (see Graham et al. 2015). Examination of stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in the muscle tissue and potential prey sources of a predatory coral reef fish has demonstrated the dietary adaptability of a predator when environmental changes rendered their usual prey unavailable (Hempson et al. 2017). Furthermore, stable isotope analysis can offer an advantage over more conventional instantaneous means of dietary sampling, such as gut content analysis and food source surveys, as stable isotopes reflect dietary sources consumed over temporal scales of weeks to months (see Costalago et al. 2012). Thus, this study used the stable isotope signatures of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) as environmental tracers, to investigate whether environmental differences among and within islands in the Philippines resulted in dietary plasticity of fish species that are both economically important for fisheries and ecologically important for coral reefs.

Specifically, I aimed to: 1) use environmental indicators of sedimentation rates and $\delta^{15}N$ isotopic signatures in the seaweed *Sargassum*, to establish whether terrestrially derived sediment (and as a proxy, nutrient) inputs onto coral reefs varied among six sites across three islands in the Philippines, 2) determine whether environmental differences among sites related to differences in food source productivity or availability, and 3) investigate whether a macroalgal browsing fish, an algal cropping fish, and a nominally planktivorous fish species suspected to consume algae, have different primary food sources under different environmental conditions and resource availabilities.

5.3 Materials and methods

5.3.1 Study sites

This study was conducted from April to June 2017, in the Central Visayas, Philippines, where there are coral reefs associated with a variety of island types with varying degrees of human occupation and influence. Six sites were selected to represent either high or low terrestrial input potential onto adjacent reefs (Fig. 5.1). These sites were selected based on surveys of in-water visibility, taken along transect lines (see Chapter 3).

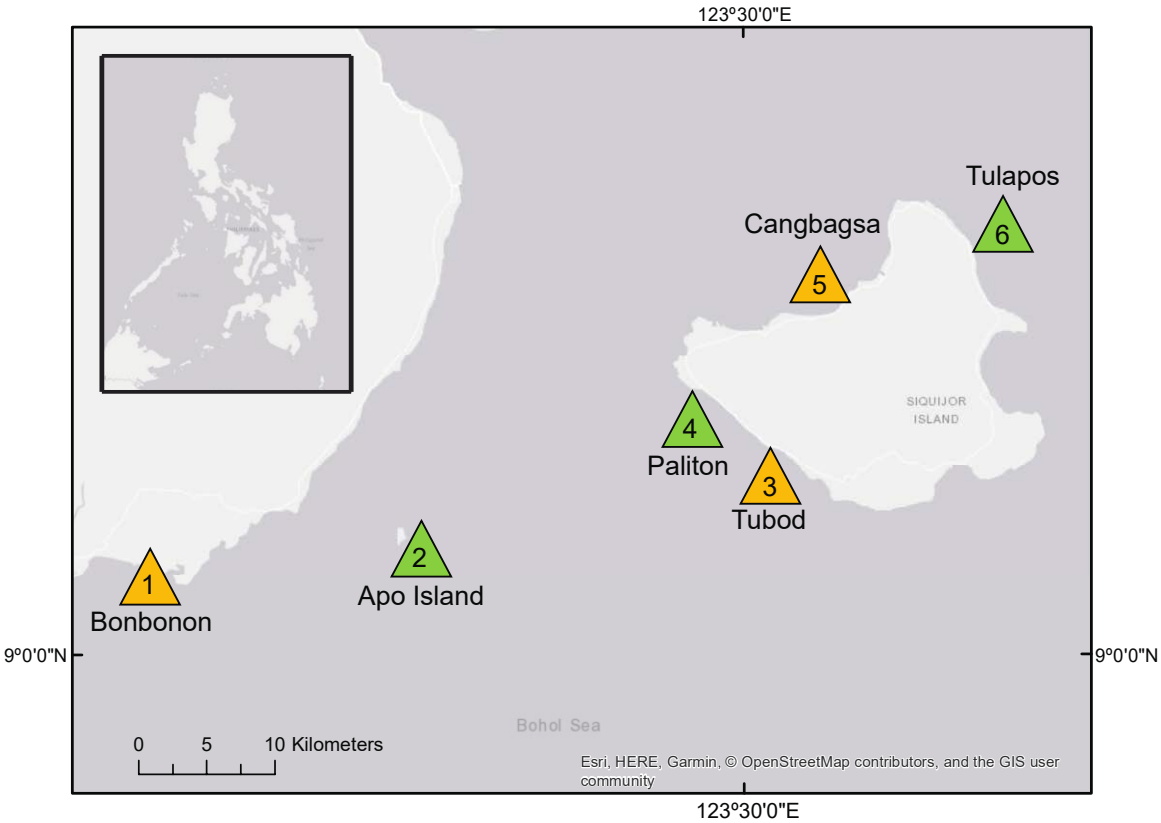

Figure 5.1. Six experimental sites on coral reefs exposed to high (orange triangles) or low (green triangles) terrestrial input of sediment and nutrients.

Potentially high terrestrial input sites were 1. Bonbonon (average in-water visibility 9.50m ± 0.90m s.d.), 3. Tubod (12.50m ± 0.86m), and 5. Cangbagsa (12.50m ± 1.83m). Low terrestrial input sites were 2. Apo Island (average in-water visibility 22.75m ± 2.67m), 4. Paliton (15.25m ± 1.18m), and 6. Tulapos (18.00m ± 2.89m). Sedimentation rates were compared among sites to confirm differences of the relative inputs of

terrestrially derived sediment using sediment traps. Environmental differences among sites were further investigated by comparing ^{15}N enrichment in the macroalgae *Sargassum* (as per Alquezar et al. 2013), and turf algal productivity and biomass (Russ and McCook 1999), as a proxy of nutrient availability among sites.

5.3.2 Estimating environmental differences among sites

Sediment traps

Sedisample® suspended sediment samplers (Stevens T 2013), herein referred to as sediment traps, were used to quantify differences in sediment input among sites. Three replicate sediment traps were deployed on the forereef of each site at depths of 5-10 m. Traps were attached to a 1.5 m steel picket driven vertically into sandy benthos and positioned approximately 1 m above the benthos. Traps were set 2-5 m apart. The deviation of the trap angle from vertical (0º) was measured using a plumb weight fixed to a protractor, to later correct for increased sediment flux with trap tilt (Gardner 1985). Sediment samples were collected eight weeks after installation (±4 days, sediment weight standardised to 57 days) using a 1-litre sample bottle attached at the base of the trap. Collected sample bottles were stored at a temperature of ~5ºC for three days to allow complete resettlement of the sediment sample. Salts were removed from the sample by decanting off saline water to the level of the precipitate, rinsing the sample in fresh water within the bottle, and repeating this procedure three times until water reached neutral salinity. Sediment was dried at 60ºC for a minimum of 48hrs or until constant weight was achieved. The three traps at Bonbonon (Site 1) were partially blocked due to accumulation of muddy sediment stuck to the inside of the traps, at the join between the trap and the sample bottle. This resulted in partial loss of the sediment sample from two traps, and almost complete loss from one trap. Sediment samples from Bonbonon were

thus removed from the analysis. However, the nature of sediment accumulation in the traps confirms the impression of high terrigenous inputs at Bonbonon.

Sargassum sampling (environmental indicator ($\delta^{15}N$), and dietary source ($\delta^{13}C$, $\delta^{15}N$))
Three whole *Sargassum* sp. thalli were collected on the reef flat adjacent to each site (except Apo Island, where *Sargassum* is known to occur (Yambao et al. 2001), but could not be found at the time of sampling). *Sargassum* thalli free of epiphytes were preferentially selected. Samples were rinsed in fresh water, stored in individual clip seal bags, then frozen. Samples were dried at 60ºC for 48 hours or until constant weight was reached. Up to twenty dried blades with small segments of attached stipe were taken from each dried sample, ensuring that both older and newer growth was sampled.

Turf algal sampling (environmental indicator (biomass), and dietary source ($\delta^{13}C$))
Experimental tiles of 10 x 10 x 1.75cm were cut from commercially available calcium carbonate tiles (as per Russ and McCook 1999). Thirty tiles were deployed at each site, attached to bare reef substrata on the forereef in depths of 4-7 m, following the depth contour of the reef to reduce variability in exposure to light and temperature conditions among tiles. Tiles were fixed to reef pavement via stainless-steel baseplates. Baseplates comprised a 10 x 3 x 0.2cm plate of stainless steel, drilled with three holes; 2 x 0.5cm diameter holes at each end to attach baseplates to reef pavement via masonry push mounts, and a 1 cm diameter hole in the centre to accommodate a bolt onto which the tile was secured. All tiles were left to condition (establish a microbial community and standing crop of turf algae) for two weeks, at which time 10 tiles were collected (initial "standing crop" treatment) and processed (see below), 10 tiles were caged ("caged" treatment), and the remaining 10 tiles left uncaged ("uncaged" treatment). Cages were

made of thin gauge (2mm) plastic chicken mesh, with a mesh size of 1.25 x 1.25cm that completely encompassed tiles to prevent grazing by large herbivores such as fish and urchins. While grazing by mesofauna such as amphipod crustaceans can be significant in coral reef systems (Brawley and Adey 1981) such organisms could not be excluded by cages from experimental tiles. However, as cages would not exclude small-bodied and juvenile wrasses (Labridae) that likely feed on such mesofauna, any effect of amphipods was considered ubiquitous across study sites and tile treatments. Tile treatments were semi-randomly allocated among the tiles at each site, with each treatment occurring every 3-4 tiles along the contour of the reef. After six weeks under treatment (eight weeks total time ±4 days), caged and uncaged tiles were photographed, removed from the reef, placed in individual ziplock bags and sealed, and refrigerated/frozen until processing. To process, tiles were rinsed with freshwater to remove detritus and salt. Detritus was isolated on plankton mesh (64µm), placed in vials and frozen for stable isotope dietary analysis. Tiles were scraped with a paint scraper for one minute to remove all growth. Large pieces of grit, molluscs, crustacea and encrusting organisms were removed from the sample at this time. Turf algal samples were rinsed in fresh water on plankton mesh (64µm), placed in vials and frozen for both productivity analysis (from biomass), and stable isotope analysis. Detritus and algal turf samples were dried at 60ºC for 48 hours or until constant weight was reached.

5.3.3 Stable isotope sampling

Three coral reef associated fish species were chosen due to their known dietary preferences, their prevalence among study sites, and their availability and importance in local commercial or subsistence fisheries (Abesamis et al. 2006, Padin et al. 2013, Abesamis et al. 2015). These fish species were a macroalgal browser, *Naso unicornis*

(Choat et al. 2002), an algal cropper, *Siganus virgatus* (Hoey et al. 2013, Plass-Johnson et al. 2015, Bauman et al. 2017), and a schooling planktivore suspected to eat benthic macroalgae, *Naso minor* (Randall 1986). Turf algae and associated detritus from experimental tiles, the macroalgae *Sargassum*, and plankton, were chosen as potential dietary sources of these three fish species. Tissues were collected from fish and potential dietary sources from April to June, at the end of the cool dry season (Amihan) in the Philippines, and immediately preceding the onset of the summer wet season (Habagat). The dry season was sampled preferentially due to the relatively calm weather and thus the ease of accessibility of shallow reef experimental sites and fisheries, compared to the wet season when prevailing wind conditions make many reef areas unworkable. Furthermore, sampling at the end of the dry period allowed the environmental signatures of much of the dry season (~4 months duration) to accumulate in fish and *Sargassum* tissues, and eight weeks of dry season environmental signature to accumulate in turf algae during the experimental period. Turnover rate of $\delta^{15}N$ in muscle tissue of medium-sized tropical reef fish is approximately three to four months (Matley et al. 2016), *Sargassum* approximately three to six months depending on the length of the growing period (Atewebrhan et al. 2005), and up to several months in large zooplankton (see McClelland et al. 2003). Marine algae (including turf algae from experimental tiles) and plankton were collected from all six sites within a period of two weeks to minimise temporal and seasonal variation in source tissue turnover, with collections timed to complement the accumulation of source signatures in fish consumer tissue. Fish tissue collections were dependent on local supply of fish, which were collected from Sites 1-5 only (Fig. 5.1) during a sampling period spanning four weeks (22 May–19 June 2017), beginning at week six of the eight-week turf tile installation. No fish were collected from Site 6 (Tulapos).

Sampling of dietary sources

Collection methods for turf algae and associated detritus, and *Sargassum* used for stable isotope analysis are described in the previous section. Zooplankton was sampled in the upper 5 m of the water column above reef slopes at each site. Zooplankton samples were collected from three replicate 5-minute horizontal tows of a 100µm mesh, 50 cm diameter plankton net, at 3-5 m depth. Contents of the net cod end were emptied onto 64µm plankton mesh sieves, collected into vials with seawater, and kept on ice. Salts were removed from samples by rinsing on sieves with fresh water. Samples were transferred to vials and frozen. Plankton samples were dried at 60ºC for 24 hours or until constant weight was reached.

Fish tissue sampling

Muscle tissue from *Naso unicornis* (*n*=29), *Naso minor* (*n*=51), and *Siganus virgatus* (*n*=83) was sampled from fisheries operating adjacent to each experimental site (Supplementary Table S5.1). No fish were sampled from Tulapos (Site 6). *Naso minor* was collected from Sites 1-4 only. *N. minor* samples from Site 3 (Tubod) and 4 (Paliton) were pooled due to the nature of fish collection, via nets set off the reef that fishers operated via boats working between the two sites. Fish were collected with spear (*N. unicornis*, *S. virgatus*) or net (*S. virgatus*, *N. minor*) and stored on ice. Each fish was measured (fork length (FL)) and weighed to the nearest gram. A 2cm x 1cm piece of dorsal muscle tissue was dissected, skin removed, and the tissue was rinsed in filtered water and frozen in 5ml sample vials. Otoliths were removed to determine the age of fish, with age considered in combination with fish body size to account for life stage. Muscle tissues were dried at 60ºC for at least 48 hours or until constant weight was reached.

Otolith processing and interpretation

The age of each individual fish was estimated from analysis of the microstructure of sagittal otoliths. Sagittae were removed from each individual, cleaned and stored dry. One sagittal otolith of the pair was then weighed to the nearest 0.0001 mg and affixed to the edge of a glass microscope slide using a thermoplastic glue (Crystalbond 509), with the primordium located just inside the edge of the slide and with the sulcul ridge perpendicular to the slide edge. Mounted sagittae were then ground down to the nucleus using a 1200-grit diamond lapping disk on a GEMMASTA lapping machine, cooled with constant cold water flow. Sagittae were then re-affixed to a secondary slide with the newly sectioned surface positioned flat against the slide and ground down to form a thin transverse section (≈200μm thick) containing the sagittal nucleus. Transverse sagittal sections were later covered with a thin layer of Crystalbond to improve optical clarity and interpretation. Ground otoliths were examined under both high-power and dissecting microscopes using transmitted light. Each otolith was viewed "blind" by two trained readers and the number of annuli recorded. When ages for an individual fish differed between readers, a third count was performed by a third independent reader and final age was assigned when at least two counts agreed.

Stable isotope analysis

Dried food source (i.e., plankton, *Sargassum*, turf algae, and detritus) tissues and consumer (i.e., fish) muscle tissues were each homogenized using a rock mill and associated mortar and pestle, in preparation for elemental (C, N) and stable isotope ($\delta^{13}C$, $\delta^{15}N$) analysis. Food source samples were subdivided into two portions, with one portion acidified with 1% hydrochloric acid to remove inorganic carbonates (Ng et al. 2007, Carassou et al. 2008), which can interfere with $\delta^{13}C$ signatures. Acidifying samples

deleteriously modifies $\delta^{15}N$, thus one portion was run to obtain $\delta^{15}N$, the second portion acidified then run to analyse for $\delta^{13}C$. Consumer muscle samples were not pre-treated to remove lipids, as chemical lipid extraction can reduce C:N ratios (Matley et al. 2016), cause $^{15}N/^{14}N$ fractionation (Sotiropoulos et al. 2004) and result in higher $\delta^{15}N$ values (Yurkowski et al. 2015). Muscle tissue generally has a lower lipid content than other tissues (Matley et al. 2016). Furthermore, if C:N ratios are ≤3.5, it is considered unnecessary to extract lipids (Post et al. 2007). All samples were weight-calibrated to run against standard reference material: 2 mg for fish tissue, 5 mg for turf algae, macroalgae and plankton. All samples were weighed into tin caps and analysed for stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) using a continuous flow Isotopic Ratio Mass Spectrometer (Europa Scientific Integra IRMS), equipped with an elemental analyser, at the Advanced Analytical Center, James Cook University, Cairns, Australia. Results are expressed in standard δ unit notation as:

$$\delta X(‰) = [(R_{sample} / R_{standard}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N, and R is the ratio of carbon ($^{13}C/^{12}C$) or nitrogen ($^{15}N/^{14}N$). Snake muscle tissue, chiton, internal C3 plant standard, and blanks were used as consumer standards. Snake muscle tissue, chiton, protein standard, and blanks were used as source standards.

5.3.4 Data analysis

Sedimentation and Sargassum $\delta^{15}N$ as indicators of nutrient enrichment

Linear models were used to compare sedimentation rates and concentrations of $\delta^{15}N$ isotopes in *Sargassum* (independently) among sites. Linear regression was used to test

the response of *Sargassum* $\delta^{15}N$ to sedimentation rate. All data were modelled with a gaussian error distribution. Models were validated through standard protocols (examination of residuals, model fit, dispersion). For models testing the categorical predictor of site, post-hoc Tukey's tests were applied to tease apart significant differences of each fitted response variable among sites. For the continuous predictor of sediment weight, a multiple R^2 value, y-intercept and slope were calculated. All analyses were performed in R with RStudio interface (Team RC 2016). Linear models were fit using the lm function, Tukey's tests were performed with the multcomp package and glht function.

Turf algal biomass, productivity, and yield to grazers

Turf algal dry weight (g) was standardised by number of days in treatment (14 days initial standing crop, 43 days caged and uncaged), and converted from grams per $0.01m^2$ (tile area) to grams per 1 m^2. Generalised linear models (GLMs) were used to test the response of turf algal biomass (g m^2) to the predictors of tile treatment (initial standing crop, caged, and uncaged), and site. Turf algal biomass was modelled with a gaussian error distribution. Both additive and multiplicative candidate models were run, and model selection made using Akaike Information Criterion (AIC), corrected for small sample sizes (AICc). Models were validated through standard protocols (examination of residuals, model fit, dispersion, autocorrelation). Model estimated means and 95% confidence intervals were calculated for final models. From the best model, turf algal productivity in absence of grazers, and turf algal yield to grazers, was calculated at each site. Productivity was estimated as the difference between mean caged turf algal biomass and the mean initial standing crop biomass. The yield to grazers was estimated as the difference between mean caged biomass and mean uncaged biomass (Russ and McCook,

1999). Post-hoc 'planned comparisons' via selective matrix multiplication were used to calculate this difference between estimated means (among sites for the same tile treatment, or within site for different tile treatments) with 95% confidence intervals calculated. Differences among sites/treatments were calculated as not significant when confidence intervals pass "0". GLMs were fit using the glm function in R with RStudio interface (Team RC 2016).

Refinement of fish stable isotope data

Many species of planktivorous surgeonfish exhibit an ontogenetic shift in diet from herbivory to planktivory with size or age (Green and Bellwood, 2009). Thus, to ensure differences in fish isotopic signatures were representative of shifts in fish diet with location, and not due to shifts in fish diet due to body size or age, only samples from fish identified as being ≥one year old were included in analysis, to eliminate crude dietary ontogenesis. Similarly, samples from fish that were juvenile in appearance (small body size, underdeveloped head morphology) were removed from analyses. Samples with C:N ratios >3.5 were removed prior to data analysis, as high lipid content of samples can interfere with isotopic signatures (Post et al. 2007). This left a total of 27 individuals of *Naso unicornis* (low input sites n=15, high input sites n=12), 41 individuals of *Naso minor* (low input sites n=19, high input sites n=13, in-between n=9), and 81 individuals of *Siganus virgatus* (low input sites n=33, high input sites n=48) (Supplementary Table S5.1).

Stable isotopes: fish diet with body mass and length

Fish body size can influence the fractionation values of $\delta^{13}C$ and $\delta^{15}N$ (Sweeting et al. 2007). Fish body size can also be used to test for ontogenetic shifts in diet (Carassou et al.

2008, Plass-Johnson et al. 2013) so linear regression (as per previous section) was used to test for the effect of body mass (g) and length (FL) on isotopic signatures.

Stable isotopes: fish diet with site

A four-source mixing model using stable isotope analysis in R (siar: Parnell and Jackson 2013) was run to estimate the proportion of each dietary source in the tissue of *Naso unicornis*, *Naso minor* and *Siganus viragtus*. Mill et al. (2007) found the $\delta^{15}N$ fractionation in herbivorous fishes differs from carnivorous species by having an elevated $\delta^{15}N$ fractionation (4-5% compared to 2-3%, respectively). However, because fractionation values specific to the consumers and sources used in this study were not available for the study region, and because I was specifically interested in testing for dietary plasticity in these consumers, I assumed diet-tissue discrimination factors of 3.54% ± 0.74(sd) for $\delta^{15}N$, and 1.63% ± 0.63(sd) for $\delta^{13}C$ (Inger et al. 2010). Diet-tissue discrimination factors were added to the source sample signature, as per the SIAR V4 handbook (Inger et al. 2010). Exploration plots of source and consumer means were produced to visualize consumer orientation within source convex hulls before siar models were run. None of the source samples were combined due to their distinctness in isotopic space, and the small number of source categories collected (Phillips et al. 2014). Models were based on 500,000 iterations with a 50,000 iteration burn in, of all food sources for each fish individual within a group (collection site) (Inger et al. 2010).

5.4 Results

5.4.1 Variation in environmental conditions among sites

Sedimentation rates

Sedimentation rates varied among sites (estimate: 0.012 ± 0.001 se, t-value: 7.679, Pr(>|t|) <0.001; Fig. 5.2a, Table S5.2), with generally higher sedimentation rates at sites with low in-water visibility, and low sedimentation rates at sites with high in-water visibility (Fig. 5.2a).

Sedimentation rate – Sargassum $\delta^{15}N$ relationship

Sargassum ^{15}N enrichment varied among sites (estimate: 4.83 ± 0.094 se, t-value: 51.27, Pr(>|t|): <0.001), was generally greater at the high terrestrial input sites than the low terrestrial input sites (Table S5.2) and showed a similar pattern of variation as sedimentation rate for each site (Fig. 5.2b). There was a significant positive relationship between *Sargassum* $\delta^{15}N$ values and sedimentation rates at sites ($R^2 = 0.66$, y-intercept = 3.2182, slope =1.4124, P<0.001) (Fig. 5.2c). *Sargassum* was not collected from Apo Island.

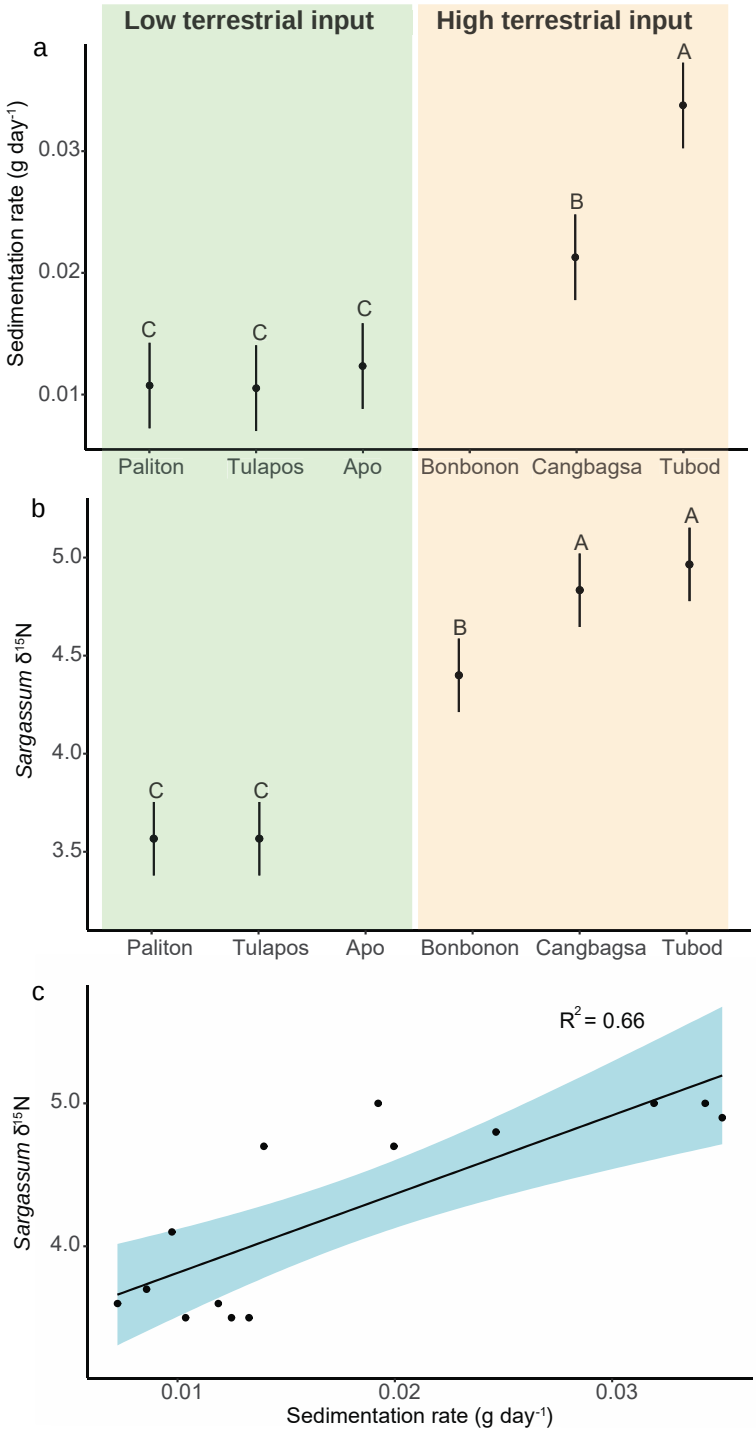

Figure 5.2. a) sedimentation rate (g day^{-1}), b) *Sargassum* δ^{15}N among sites, and c) the sedimentation rate - *Sargassum* δ^{15}N correlation. In a) and b) letters indicate a significant difference among sites, with unique letters being significantly different from each other and like-letters not being significantly different (Table S5.2). Error bars are 95% confidence intervals. Note that sediment samples were lost from Bonbonon, and *Sargassum* could not be found and was thus not collected from Apo Island. In c) the relationship between *Sargassum* δ^{15}N (y-axis) and sedimentation rate (g day^{-1}) (x-axis) with fit (solid black line) and 95% confidence intervals (blue shaded area).

Sedimentation rate, turf algal biomass, productivity and yield to grazers

There were significant differences in the biomass of turf algae among sites (estimate: 12.33 ± 6.13 se, t-value: 2.01, Pr(>|t|): 0.046) (Figure 5.3a, Table S5.3), and within sites between caged and initial standing crop treatments, and uncaged and caged treatments (Caged–Standing Crop: 26.45 ± 8.45 se, z-value: 3.12, Pr(>|z|): 0.005; Uncaged–Caged: -22.66 ± 8.04 se, z-value: -2.818, Pr(>|z|): 0.0134). There was no significant difference between uncaged and initial standing crop treatments at any site (Uncaged–Standing Crop: 3.79 ± 8.27 se, z-value: 0.458, Pr(>|z|): 0.89 NSD). Caged tiles had significantly more turf algal biomass than uncaged tiles, except at two high terrestrial input sites (Bonbonon and Cangbagsa) where algal turf productivity was generally low. The sites furthest from shore (Paliton), and the site associated with a tourist resort (Tubod) had the highest productivity of algal turfs.

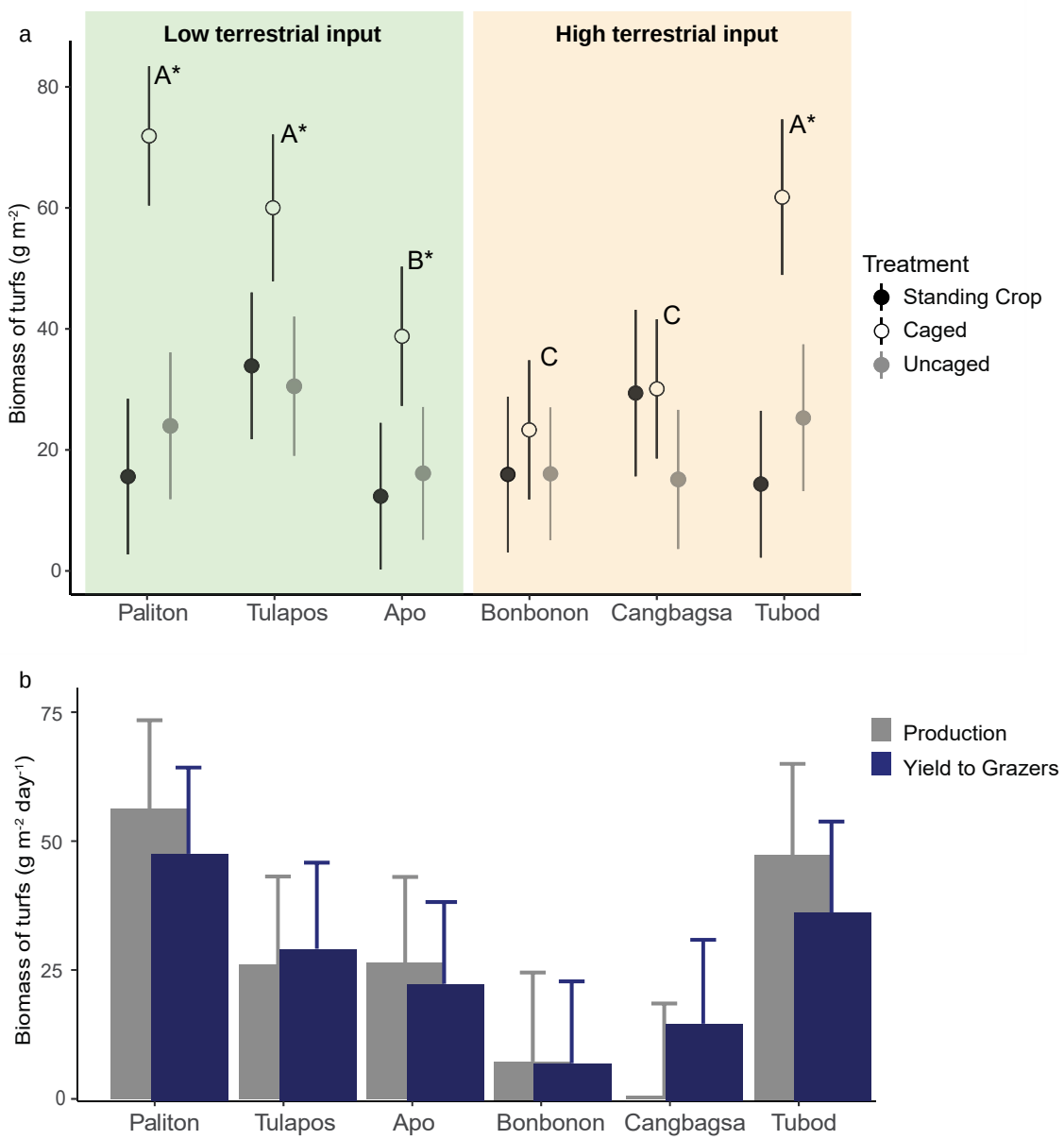

Figure 5.3. a) Turf algal biomass (g m^{-2}) among sites and experimental tile treatments. Points represent modelled mean estimates of turf algal biomass (g m^{-2}) with 95% confidence intervals. Letters indicate significant difference among sites for caged treatments only, with unique letters being significant from each other and like-letters not significantly different from each other, based on planned factor comparisons of a general linear model (Table S3). Asterisks indicate significant differences between caged and uncaged treatments for each site. There was no significant difference between uncaged and initial standing crop treatments at any site. b). Estimated mean algal turf production (grey, n=10) and yield to grazers (navy blue) (g m^{-2} day^{-1}) at each site, with 95% confidence intervals.

5.4.2 Stable isotope analysis

Stable isotopes: $\delta^{13}C$ *and* $\delta^{15}N$ *variability with consumer body mass and length*

There was a weak but significant positive relationship between the $\delta^{13}C$ isotope in fish muscle tissue, and fish body size (mass and fork length) for *Naso unicornis* and *Naso minor*, but not for *Siganus virgatus* (Table 5.1). There was a weak but significant positive relationship between the $\delta^{15}N$ isotope in fish muscle tissue and body size (mass and fork length) for *Siganus virgatus*, but not for *Naso unicornis* and *Naso minor.* Age ranges of these species were, *Naso unicornis*: 1-12 years, *Siganus virgatus*: 1-7 years, and *Naso minor*: 1-11 years.

Table 5.1. Stable isotope relationships with fish size

Species	***n***	**Diet Group**	**Predictor**	**Stable Isotope**	**Slope**	**y-Intercept**	**R2**	***p***
Naso unicornis	29	Browser	Fork Length (mm)	$\delta^{13}C$	-0.005	-9.400	0.159	**0.036**
				$\delta^{15}N$	0.002	6.581	0.058	0.217
			Mass (g)	$\delta^{13}C$	-0.001	-10.070	0.141	**0.049**
				$\delta^{15}N$	0.001	6.784	0.096	0.109
Siganus virgatus	82	Grazer	Fork Length (mm)	$\delta^{13}C$	0.008	-15.572	0.029	0.125
				$\delta^{15}N$	0.009	5.454	0.072	**0.015**
			Mass (g)	$\delta^{13}C$	0.003	-14.636	0.025	0.156
				$\delta^{15}N$	0.003	6.527	0.053	**0.038**
Naso minor	42	Planktivore	Fork Length (mm)	$\delta^{13}C$	0.006	-18.617	0.185	**0.005**
				$\delta^{15}N$	0.003	9.034	0.025	0.319
			Mass (g)	$\delta^{13}C$	0.003	-17.850	0.207	**0.002**
				$\delta^{15}N$	0.003	9.355	0.065	0.103

Stable isotopes: food source contribution to consumer diets

The four potential food sources were located distinctly in isotopic space, covering a wide range of values for both $\delta^{13}C$ and $\delta^{15}N$ (Fig. 5.4). Turf algae was the most depleted in $\delta^{15}N$ and enriched in $\delta^{13}C$, with an almost step-wise progression in enriching $\delta^{15}N$ and depleting $\delta^{13}C$ for detritus, *Sargassum* and plankton, respectively (Fig. 5.4). Each species of fish consumer sat distinctly in isotopic space relative to the positions of the potential dietary sources, suggesting difference in diet among species. There was not a clear separation of fish 'Groups' (by site) for each species (except *N. unicornis* Group 2, Apo Island), suggesting little or no difference in the diet of each species among sites. Stable isotope mixing models run on food sources for each consumer at each site indicated that there was variation in the percent contribution of sources to consumer diet among sites, however this was not significant for any fish species, nor any site (Fig. 5.5, Table S5.4).

N. unicornis at the low terrestrial input site, Apo Island (Group 2), appeared to sit more distinctly in isotopic space than *N. unicornis* from other sites (Fig 5.4a), however the proportion of sources in the diet of *N. unicornis* were not significantly different at any site. *Naso unicornis* was eating turf at all sites but not significantly more turf at any site (Fig. 5.5a, Table S5.4). The lowest proportion of turf consumed by *N. unicornis* was at the high terrestrial input site of Bonbonon (mode: 31%, lower and upper 95% credible interval [3-57%], Table S5.4), with the highest proportion at the low terrestrial input site of Paliton (57% [40-72%]). *N. unicornis* was likely eating *Sargassum* at all sites, but the model indicated uncertainty in the proportions of *Sargassum* in diets at all sites except Apo Island (31% [1-48%], Table S5.4), where *Sargassum* could not be found at time of sampling. *N. unicornis* was unlikely consuming plankton at any site (mode range: 1-4%, lower CI=0, Fig. 5.5a, Table S5.4).

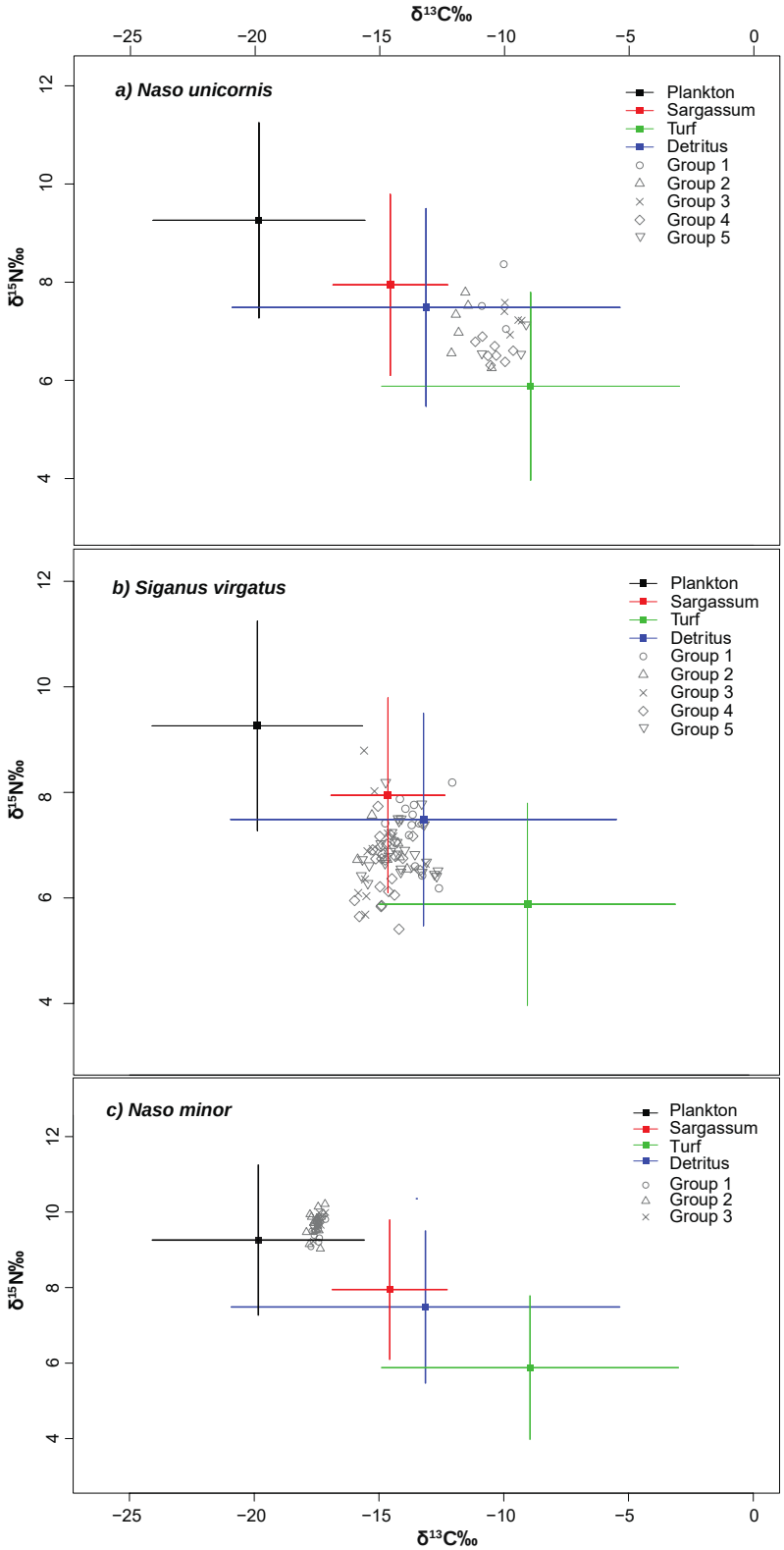

Figure 5.4. Sample $\delta^{15}N$ (x-axis) vs. $\delta^{13}C$ (y-axis) biplots of consumers a) *Naso unicornis*, b) *Siganus virgatus*, and c) *Naso minor*, and their potential food sources corrected for trophic enrichment. Food sources are means with 95% confidence intervals. Groups 1-5 are sites 1. Bonbonon, 2. Apo, 3. Tubod (Tubod and Paliton combined for *N. minor*), 4. Paliton, 5. Cangbagsa. Each point within a Group is an individual fish

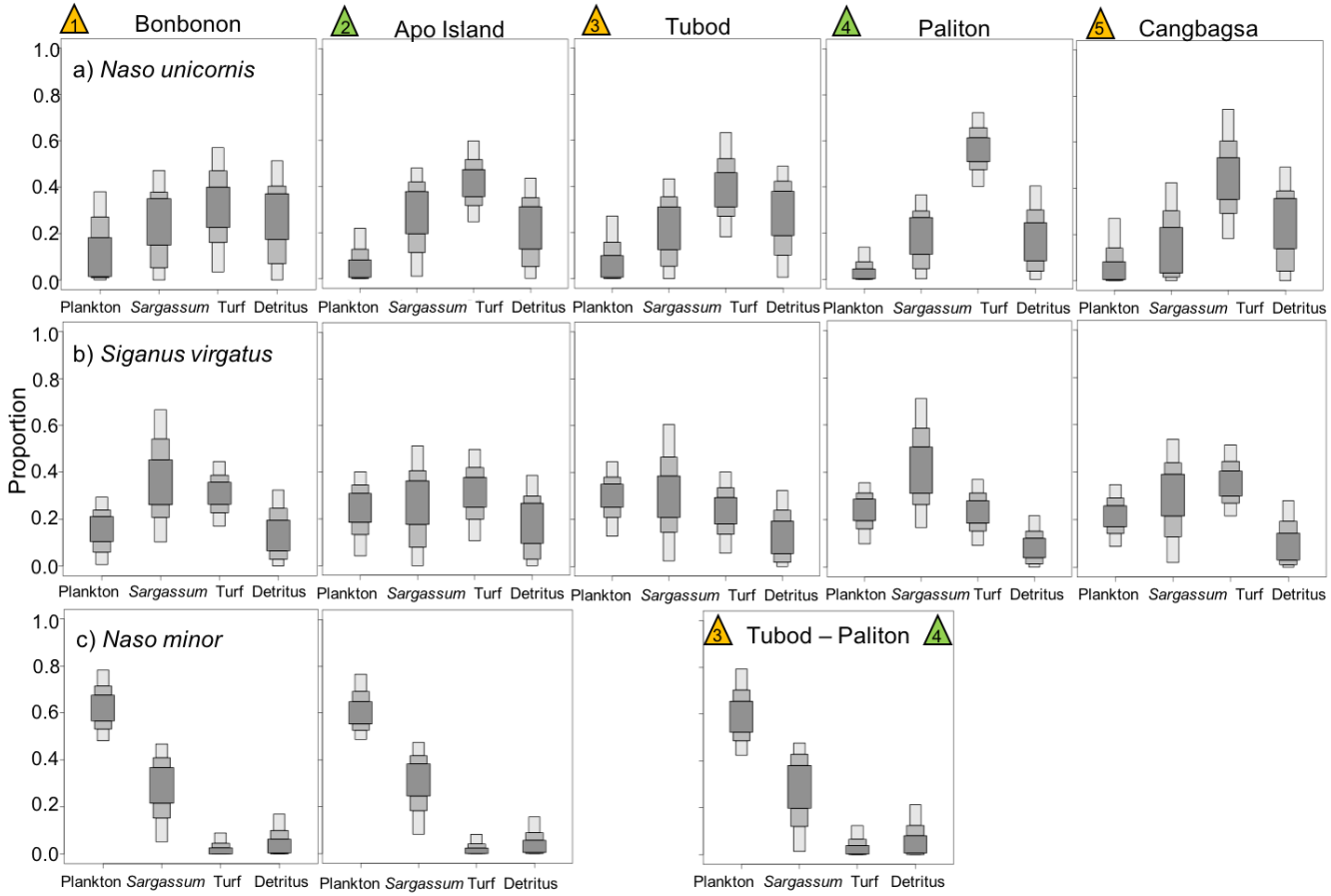

Figure 5.5. The proportional contribution of food sources to the diets of each consumer species among sites 1. Bononon, 2. Apo, 3. Tubod, 4. Paliton, 5. Cangbagsa. Sites 3-4 are combined for *Naso minor* as fishing gear sampled both together. Proportions with 25% (dark grey), 75% (medium grey) and 95% (light grey) credibility interval (CI) levels. Lower limits of CIs give confidence in proportional contribution. e.g. Lower 95% CI >0.0 indicates the source is contributing to consumer diet (within the bounds of CIs). Lower 95% CIs touching zero indicates uncertainty on the proportional contribution of a source. Lower 25% CIz touching zero the source is unlikely contributing to the diet of the consumer. Refer to Table S5.4 for siar model outputs for each species.

Siganus virgatus was consuming *Sargassum* at four of five sites (mode range: 29-40% [2-71% CI], Table S5.4), but there was uncertainty in the proportion of *Sargassum* consumed at the low terrestrial input site of Apo Island (mode: 28% [0-51%]), where *Sargassum* could not be found at time of sampling. *Siganus virgatus* was consuming filamentous turfs (mode range: 23-34%) at each site, with similar proportions among sites (Fig. 5.5b, Table S5.4). There was no significant difference between *Sargassum* and turf in the diet of *S. virgatus* at any site. The model was confident that *S. virgatus* was eating plankton at all sites, with the smallest proportional contribution at high terrestrial input site of Bonbonon (mode: 15% [1-29%]) and greatest proportion to diet in the high terrestrial input site of Tubod (mode: 31% [13-45%], Table S5.4) but the plankton contribution to the diet of *S. virgatus* was not significantly different at any site.

The diet of *Naso minor* was dominated by plankton at each site (mode range: 60-62% [42-79%]) with no significant difference in the proportion of plankton in the diet among sites (Fig. 5.5c, Table S5.4). *Sargassum* contributed to the diet of *N. minor* at all sites (mode range: 28-31% [1-47%]. *N. minor* was not likely consuming detritus or turfs at any site.

5.5 Discussion

Despite differences in environmental conditions among sites, and differences in the content, biomass and productivity of potential food sources among sites, stable isotope analysis indicated that the diets of three fish species did not differ among sites. There was a strong positive relationship between sedimentation rate and $\delta^{15}N$ values in *Sargassum,* indicating differences in the uptake of nutrients by *Sargassum* among sites

(Alquezar et al. 2013, see also Graham et al. 2015). Conversely sites that had high sedimentation rates appeared to have less turf algal biomass, productivity, and yield to grazing fishes, potentially limiting food availability to grazing fishes (including croppers such as *Siganus virgatus*) (Tebbett et al. 2018). Yet there were no significant differences in the proportion of the four dietary sources of plankton, *Sargassum*, turf algae and detritus in the stable isotope signatures of the macroalgal browser *Naso unicornis*, the algal cropper *Siganus virgatus,* and the planktivore *Naso minor*. Why did these differences in environmental conditions among sites not lead to a significant difference in food intake of fish among sites?

Potentially, the differences in environmental condition among sites were not great enough to significantly alter availability of food sources. If all primary food sources were available to consumers at each site throughout the study period, one might not expect to see significant differences in the proportions of dietary sources in the tissues of fish consumers. While there was generally lower turf algal growth under higher sedimentation rates, there was not a complete absence of growth. These differences were reflected in the diet of the macroalgal browsing species, *N. unicornis*, that had proportionally less turf algae in its diet at Bonbonon where turf algal growth was depressed, and proportionally more at Paliton where turf algal growth was high, but not significantly more or less at any site. Conversely, the cropping species *S. virgatus* was eating almost equal proportions of algal turfs among sites irrespective of relative supply or sedimentation rates. Grazing fishes (including croppers) have been shown to avoid sediment laden turfs (Bellwood and Fulton 2008), but even relatively high, natural sedimentation rates may not deter grazing fishes completely (see Tebbett et al. 2018), as indicated here. Turf algal growth appeared to have a complex relationship with

sedimentation rate in this study, with the highest sedimentation rate site of Tubod also having a high turf biomass. This was potentially due to nutrient inputs from an adjacent resort, evidenced by the highest $\delta^{15}N$ values of any site. A similar trade-off between sediment suppression and nutrient enhancement of algal turfs under relatively high sediment conditions has been seen on the inner-shelf Great Barrier Reef (GBR). On the inner-shelf, turf algal production and yield to grazers was generally low compared to the mid- and outer-shelf GBR, however, when a cyclone resuspended nutrients from soft sediment substrata near inshore reefs, algal turfs on these inner-shelf reefs had comparable productivity to turfs on mid- and outer-shelf reefs (Russ and McCook 1999). Unlike the GBR where macroalgae such as *Sargassum* is prevalent, largely only on inner-shelf reefs (McClure et al. 2019), *Sargassum* is present at all sites in the study region, including the clear water, low sedimentation site at Apo island (Yambao et al. 2001), despite the inability to find it for collection at the time of this study.

Seasonal variation in food availability may have an effect on consumer dietary plasticity. Both the abundance and nutritional quality of seaweeds has been shown to vary among seasons, in both temperate (Horn and Neighbors 1984) and tropical regions (Lefe`vre and Bellwood 2010), potentially influencing the feeding preferences of herbivorous fishes. For example, a temperate herbivorous fish, *Odax pullus*, preferentially fed on the reproductive structures of a fleshy macroalgae when seasonally available (Clements and Choat 1993). Tropical herbivorous fishes feed less on *Sargassum* during the Austral winter on the GBR due to condition of *Sargassum,* specifically increased epiphyte loads and decreased nutritional quality (Lefe`vre and Bellwood 2010). Seasonal switches in dietary sources have also been demonstrated in planktivorous fishes in a marine rocky reef system, demonstrated by the isotope mixing model protocol employed in this study

(Costalago et al. 2012). I sampled from April to June toward the end of the cool, relatively low rainfall season of the western Central Visayas (Abesamis et al. 2015). The seasonality of *Sargassum* spp. typically includes a period of growth, until maximum length and maturation occurs, followed by senescence, with the timing of this process being largely temperature dependent (Martin-Smith 1992, Ateweberhan et al. 2005, Fulton et al. 2014). In the central Visayas, degradation in the physical structure of *Sargassum*, leading to decreased abundance, has been observed to begin between August and October, lasting until November to February, depending on the species (Largo and Ohno 1992). Thus, potentially sampling during the hotter, relatively wetter months would see increased sedimentation in coastal areas near river mouths potentially impacting algal turf availability, and capture natural seasonal fluctuations in the availability of *Sargassum*, leading to potentially greater differences in the dietary signatures of fish consumers.

While the fish species investigated in this study did not change diet with environmental condition, analyses indicated that fish were feeding on unexpected amounts of some sources, given what is known of their ecology. For example, *Naso minor* is almost exclusively considered a planktivorous unicornfish, though there is one account of its feeding on benthic algae (Randall 1986). Little is known about the life history of this species generally (J.H. Choat, pers. comm.), which may be of concern given its frequency of capture in subsistence fisheries (Abesamis et al. 2015). Here, I provide the first account of the age range of these fishes, as quantified by otoliths, which exceeds their expected maximum age by many years (J.H. Choat, pers. comm.). *Siganus virgatus* was observed feeding in the water column on plankton at both the low input site of Paliton and the high input site of Tubod (pers. obs.). This is perhaps unusual behaviour for a

species documented as feeding largely on macroalgae (Plass-Johnson et al. 2015, Nanami 2018) and filamentous red and green algae (Fox et al. 2009, Hoey et al. 2013, based on its sister taxon *S. doliatus* (Randall et al. 1990)). Gut content analysis of the individuals of each species would help clarify the results of the stable isotope mixing model, particularly in the case of *Naso unicornis,* for which there was the most dietary uncertainty. This uncertainty indicates that I perhaps did not sample a wide enough variety of potential food sources to gain a clear understanding of the primary dietary sources of the study species (Phillips et al. 2014). Indeed, beyond feeding on *Sargassum* (Hoey and Bellwood 2010), *N. unicornis* is known to feed on other brown macroalgae such as *Turbinara* and *Dictyota* (Choat et al. 2002) and filamentous turfs (Crossman et al. 2005). Thus, extending sampling to other fleshy brown macrophytes as potential food items may produce more definitive results, but was not possible in the scope of this study.

Likely, the fish consumers investigated here either did not have the need to switch dietary sources, or their ecology does not allow it. Yet, even coral reef fishes considered as dietary specialists may exhibit some degree of dietary plasticity when their regular food source is unavailable (Feary et al. 2018). For example, the highly specialised coral feeding butterflyfish *Chaetodon octofasciatus*, exhibited prey switching and thus population persistence on highly degraded reefs that cannot sustain its regular coral prey (Feary et al. 2018). Furthermore, the generalist piscivore, *Plectropomous maculatus*, switched prey from planktonic feeding damselfish that inhabit acroporid corals, to benthic feeding herbivorous damselfish, when the abundance of *Acropora* and associated damselfishes declined following severe coral bleaching and recurrent flooding events in the Keppel Islands, GBR (Hempson et al. 2017). That species in this study did not exhibit measurable dietary plasticity is perhaps then indicative of a lack of need, rather

than a lack of ability. Indeed, given the indication of the nominally planktivorous species *N. minor* incorporating significant proportions of macroalgae into its diet, and the nominally herbivorous species *Siganus virgatus* incorporating significant proportions of plankton into its diet, suggests that these species are perhaps more opportunistic and adaptable than our traditional views of their ecology suggest. Perhaps therefore, under more severe circumstances of environmental change, dietary plasticity in these important food fish species would be observed.

Understanding how ecologically and economically important fishes persist in a variety of environmental conditions is important for long term success of fisheries and ecosystems. Results of this study indicate that the same fish species inhabiting different environmental conditions did not change primary dietary sources. This was the case despite likely differences in the availability of food sources, as evidenced by significant differences in turf algal productivity among sites, and the difficulty in sourcing *Sargassum* from Apo Island. However, while the analyses employed in this study were comprehensive, they provide only a small indication of the dietary ecology of these fishes. For example, there was some evidence that *Naso unicornis* from Apo Island may have a different diet than like-species from other sites, based on the visible separation of the Apo Island group from other groups (sites) in isotopic space. Given what is known of the diet of *N. unicornis* (Choat et al. 2002, Crossman et al. 2005), further sampling of additional macroalgal species may have given more definitive results, providing the macroalgal sources had distinct isotopic signatures (Parnell et al. 2010, Phillips et al. 2014). Collecting additional source samples was unfortunately not within the scope of this study. However, incorporating gut content analysis, behavioural feeding observations, variations in otolith growth increments, elemental analysis of carbon and nitrogen content in food source and

consumer tissues may provide further indicators of whether these fish feed on different sources, or perhaps obtain different nutritional value from the same sources, under different environmental conditions. Many of these analyses are a possibility for future directions in this work.

5.6 Conclusions

With human impacts altering sediment and nutrient regimes on many tropical coral reefs, this study provides valuable insight into the dietary flexibility of important food fish species under a variety of environmental conditions. This is particularly pertinent in developing island nations that rely on the success of multi-trophic level fisheries, yet simultaneously have a history of poor land-use practices adjacent to coral reefs that can adversely affect sediment and nutrient regimes (Hodgson and Dixon 1988, Jones et al. 2004, Halpern et al. 2013, Hamilton et al. 2017, Lamb et al. 2017). While fish did not change primary dietary sources with locations in this study, all species appeared to feed on dietary sources that were not typically characteristic of the adult diets of these species, exhibiting their ability to utilize local conditions. This study provides new insights into the feeding ecology of *Siganus virgatus*, *Naso unicornis* and *Naso minor*, an important step towards their successful management.

Chapter 6: General Discussion

Understanding how coral reef fish assemblages are influenced by fine scale habitat characteristics, occurrence of disturbance events, prevailing environmental conditions, and protection through no-take marine reserves, is essential for management. This thesis examined these themes to provide ecological insights that will improve the management of coral reef fish assemblages and associated fisheries.

Live coral cover and habitat for fishes, and indeed the destruction of live coral cover from severe disturbances, are clear drivers of fish assemblages, with numerous studies having reported changes in the density and composition of reef fish assemblages following coral loss and/or reductions in physical structure (Jones et al. 2004, Graham et al. 2006, Wilson et al. 2006; 2008, Munday et al. 2008, Pratchett et al. 2008; 2011, Adam et al. 2014, Russ et al. 2015; 2018, Hoey et al. 2016, Samoilys et al. 2018). This thesis extends on previous works to demonstrate that when severe disturbances modify coral reef habitats considerably, fish assemblages may remain distinct, but undergo shifts in species dominance (Chapter 2), and increases in biomass of nominally herbivorous fish groups (Chapter 2). Furthermore, results of this thesis showed that the responses of fish assemblages to habitat characteristics occurred irrespective of no-take marine reserve protection, thus indicating that habitat (and especially disturbance to habitat) is the stronger driver (Chapter 3-4). However, this thesis also demonstrated that no-take marine reserves continue to be effective fisheries management tools even when habitat for fishes has been severely damaged, by increasing the biomass and abundance of fishes relative to fished areas (Chapter 3). This latter result comes at an important time, as recent studies question the utility of NTMRs in light of the overwhelming nature of climatic threats to coral reefs (Bruno et al. 2019).

The different environmental conditions under which coral reef assemblages exist contribute to fish species richness and to the formation of inherently different assemblage structure of fish species among environments (Chapters 2-4, Fabricius et al. 2005, Cheal et al. 2013, Taylor et al. 2015, Neves et al. 2016, Heenan et al. 2016, Samoilys et al. 2018). Findings of this thesis build on a growing body of literature regarding the influence of environmental processes on coral reefs, but present new insights at the level of fish assemblages (Chapters 2-3), fish trophic groups (Chapter 4), and individual species (Chapter 5). Differences in environmental conditions of fish assemblages may affect their inherent susceptibility to, or recovery from, disturbances. For example, on the GBR, cross continental shelf herbivorous fish assemblages responded differently to severe environmental disturbances depending on shelf position (Chapter 2), with inner-shelf reefs having reduced species redundancy following disturbances compared to assemblages on reefs further from shore (Chapter 2). Furthermore, in the Philippines, mainland NTMRs in typhoon damaged areas had a different assemblage structure of large fishes (>10cm TL) compared to fished areas under the same conditions (Chapter 3). However, on mainland islands without typhoon damage there was no difference in assemblage structure of these fishes between NTMR and fished areas, indicating that the combination of fishing, coastal runoff, and extreme environmental disturbance may negatively interact to degrade fish assemblage structure (Chapter 3). Island-scale characteristics, including distance from rivers and island elevation, were more influential on the abundance of trophic groups of fishes than NTMR effects, irrespective of whether the fish were targeted by fishing (Chapter 4, see Heenan et al. 2016 for comparison). However, environmental differences among and within islands did not seem to influence the diet of a macroalgal browsing species, an algal cropping species, and a planktivorous species among sites (Chapter 5).

Finally, this thesis reinforces the positive response of fishes targeted by fishing to small NTMRs (Chapter 4). Results demonstrate that while the abundance of fishes targeted by fishing increases with increasing size of NTMRs, reserves as small as 15-20 hectares can have higher abundance of targeted fish (and for mesopredators and grazer/detritivores, species richness) compared to adjacent fished areas (Chapter 4). This result comes at an important time considering that marine spatial planning recommendations increasingly stress the importance of NTMRs being on the scale of 10's of kilometres minimum to achieve conservation benefits (Edgar et al. 2014, Krueck et al. 2017), a challenging expectation for most small-scale community managed initiatives where social needs and governance restrictions must also be considered (Samoilys et al. 2007, Green et al. 2014). Thus, using different sized reserves in combination to create connectivity and incorporate recent advancements in larval and adult fish movement, may be a more realistic and ecologically beneficial strategy (Green et al. 2014; 2015, Abesamis et al. 2017, Weeks et al. 2017). This knowledge, combined with the results of this thesis that small reserves provide increases in biomass (Chapter 3), abundance, and (for heavily targeted fish groups) species richness (Chapter 4) of large-bodied fishes relative to fished areas, is of great significance for the success of biodiversity conservation and fisheries management.

6.1 Implications for management

One of the strengths of this work lies in its applicability to management outcomes, particularly in developing island nations such as the Philippines. Especially pertinent is the evidence that 1. NTMRs in the Philippines remain successful as multi-species fisheries management and conservation tools, despite habitat disturbance and environmental differences among islands (Chapter 3), and despite their small size

(Chapter 4); and 2. NTMRs had a lower percent cover of macroalgae than adjacent fished areas, particularly on mainland islands, highlighting that protection of herbivorous fishes from fishing has a positive, albeit small, influence on benthos (Chapter 3, Stockwell et al. 2009). This is information that can be directly and immediately communicated to local resource managers in the Philippines to encourage the continued safe-guarding of resources through NTMRs. Additionally, discussions should be initiated with management authorities to set long-term goals for restrictions on certain fishing gear types, and/or enforcement of minimum size limits for retained fish, particularly for mesopredatory fishes, grazing and detritivorous fishes, which were found to be particularly vulnerable to fishing in the Philippines (Chapter 4).

This thesis also reinforced the great importance of habitat in determining fish assemblages (Chapters 2-4), and that habitat destruction diminishes NTMR benefit (Chapter 3, Jones et al. 2004, Halpern et al. 2016). Thus, it is essential that coastal resource management strategies begin to incorporate knowledge of regional environmental processes such as typhoon activity and sedimentation impacts, to improve the success of NTMRs, and safeguard habitat for fishes generally (this thesis, Álvarez-Romero et al. 2011, Hamilton et al. 2017). For example, establishing NTMRs in areas less exposed to typhoons where possible, particularly as part of NTMR networks, connected across ecologically meaningful spatial scales (Weeks et al. 2012, Green et al. 2015, Abesamis et al. 2017) will be important as the intensity of severe tropical storms increases (Mei et al. 2015). Furthermore, integrated land-sea management strategies to limit sediment and nutrient runoff onto coastal coral reefs, and that place new NTMRs away from likely sources of terrigenous sedimentation, would likely improve management outcomes through direct, and indirect affects (Hodgson and Dixon 1988, Fabricius 2005, Álvarez-Romero et al. 2011, Halpern et al. 2016, Wagner et al. 2016,

Babcock et al. 2016). However, no single management strategy for improving coral reef processes should be relied upon too heavily (see Babcock et al. 2016).

6.2 Future research directions and avenues for improvement

This thesis aimed to understand whether NTMRs still perform as fisheries management and conservation tools, considering the interaction of coral reef benthic and fish assemblages with prevailing environmental conditions, including those exacerbated by human influence. As with many studies, this thesis has raised many new questions and formed a sound platform for future research, in various directions. Building on the results of this thesis would improve not just our ecological understanding of what drives coral reef assemblages, but the practical applicability of this knowledge to producing sound and tangible management outcomes.

Chapter 2 showed that fish assemblages at multiple points along a persistent environmental cross continental shelf gradient respond differently to severe environmental disturbances of thermal bleaching and cyclones. Naturally, this raises the question of whether benthic and fish assemblages across the shelf will recover at the same rate, given their exposure to different environmental conditions of water quality and wave action. Thus, an obvious avenue for building on the knowledge gained in Chapter 2 is to monitor these cross-shelf assemblages into the future. Such monitoring would provide us with valuable insights into the response and recovery of coral reefs at a time of climatic uncertainty (Hughes et al. 2017; 2018; 2019). As well as monitoring fish assemblages, incorporating more detailed before-after impact comparisons of the benthic assemblages across the GBR continental shelf could improve understanding of the response, recovery and potential reorganisation of both benthic assemblages and associated fish assemblages following disturbances (Richardson et al. 2018, Mellin et al. 2019).

Chapter 3 demonstrated that no-take marine reserves can provide benefits to fisheries by having higher fish biomass relative to fished areas, despite severe typhoon damage to habitat for fishes, and despite location on mainland or offshore islands. Unfortunately, due to a lack of before typhoon impact data, and lack of temporal data generally, asking whether NTMRs might do a better job of recovering fish biomass than adjacent fished areas was not possible. Much debate remains as to whether NTMRs may (Roberts et al. 2017) or may not (Bruno et al. 2019) provide reefs with resilience to disturbance events. That is, while NTMRs cannot prevent many types of environmental disturbance, they may be able to enhance the recovery of reefs by maintaining ecosystem processes (Roberts et al.2017, Mellin et al. 2016). Thus, similarly to Chapter 2, an obvious next step is to continue to monitor the performance of typhoon damaged NTMR-fished control reefs into the future. Incorporating surveys of juvenile hard corals inside and outside of NTMRs, in areas both damaged and not damaged by typhoons, and on offshore and mainland islands, may provide indications of relative recovery of live coral cover among different reef conditions. Indeed, surveys of juvenile corals and detailed photographs were taken in 2016, forming a sound baseline on which to build a benthic recovery study.

Chapter 4 used Boosted Regression Trees (BRTs) to tease apart whether different groups of fishes responded primarily to bottom-up or top-down processes. BRTs are a powerful tool for exploring complex environmental datasets (Elith et al. 2008). However, during this study I encountered difficulties in finding appropriate error distributions to fit fish biomass data for some fish groups. Thus, only the results on fish abundance (and richness) were presented. It is important to consider the response of fish biomass to environmental variables as biomass is considered a good indicator of reserve effects, especially in terms of fisheries management, incorporating both abundance and size of

individuals into one metric (McClanahan et al. 2015). Alternatively, exploring the response of body size of target and non-target fishes is increasingly used as a suitable response metric when predicting habitat, biogeographical and fishing effects (Taylor et al. 2015, Harborne et al. 2018). Continuing with BRTs would be the preference due to their power and flexibility (Elith et al. 2008) and would be possible given the typical Poisson or Gaussian distribution of fork lengths, at least for larger bodied fishes. Likely, abundance remains the most relevant metric for small bodied fishes. Extending the analysis to include the response of a greater range of typically non-target species to habitat-, island-scale and management metrics would also be a worthy pursuit, contributing to knowledge of reef fish assemblage response to bottom-up or top-down processes (e.g. see Leahy et al. 2015a).

Furthermore, presenting multiple proxies of extraction activities by humans (top-down processes) may provide further insight into the likely anthropogenic drivers of reef fish assemblages. For example, in the absence of data on local fishing effort/intensity, incorporating human population density adjacent to fishing grounds could provide a reliable indication of potential fishing pressure when there is a high human dependency on marine resources (Newton et al. 2007, Kronen et al. 2010, Heenan et al. 2016, Cinner et al. 2018, Harborne et al. 2018). However, population density of humans is a less useful proxy of fishing pressure when motorised boats are used (Taylor et al. 2015), which likely disperses fishing effort. Nevertheless, incorporating an additional metric of fishing effects other than NTMR characteristics would be valuable. The availability of reliable human population data at the level needed for our NTMRs is problematic however, and thus will be an avenue of future exploration.

That fishes appeared not to be changing diet among sites, despite differences in environmental conditions, as found in Chapter 5, warrants further exploration. For

example, there is likely some benefit or consequence of feeding on food sources produced under different environmental conditions (see Hempson et al. 2018). Results from analysis of *Sargassum* $\delta^{15}N$ values as an environmental indicator showed variability in nutrient enrichment among sites. Thus different amounts of nitrogen were likely available (in primary source items) to the next trophic level of fishes among sites (Russ and McCook 1999, Tebbett et al. 2018). Complete elemental and isotopic analysis of turfs, plankton, detritus and *Sargassum* would help strengthen evidence of environmental differences found among sites. Furthermore, there are additional interrogations of fish consumer isotopic and biological data that could be performed to increase understanding of fish consumer interactions with their environments. Analysis of otolith increments from individuals may give some indication of growth rates under different environmental conditions (Leahy et al. 2015b, Hall et al. 2019). If individuals are gaining more or less nutritional benefit from food sources among locations, their growth rates may differ, and this may be reflected in the otolith structure. This is a relatively new area of research and poses an exciting avenue for exploration.

Incorporating gut content analysis of individuals from photographs (following classifications of Choat et al. 2002) and behavioural observations of fish feeding may further validate results from the isotope mixing model (Phillips et al. 2014). Furthermore, primary source samples were chosen based on what was known of the diet of each fish species (*Naso unicornis* – Choat et al. 2002, *Siganus virgatus* – Hoey et al. 2013, *Naso minor* – Randall 1986, Abesamis et al. 2015), preliminary observations of fish feeding among sites prior to collection (Phillips et al. 2014), and the potential food sources known be prevalent and collectable at each site. Extending the range of food source samples to incorporate additional species of brown, red and green macrophytes would have been ideal for improving confidence around stable isotope mixing model outputs. However,

the availability of another macrophyte species among all sites was limited, and financial restrictions of stable isotope analysis meant that extending sampling further was beyond the scope of the study. These limitations in source sampling mean that stable isotope mixing model results are currently indicative only, and further statistical analyses of stable isotope data may be needed prior to publication.

6.3 Concluding remarks

The outcomes of this thesis contribute to our understanding of the ecological drivers of fish assemblages under a variety of environmental and anthropogenic influences. But beyond ecological knowledge, this thesis provides highly applicable information with which to improve management of coral reefs that so many people rely upon as a resource. No-take marine reserves remain an important, simple tool in an array of coral reef management strategies, particularly within subsistence fisheries in developing nations. However, throughout this work, it was evident that maintaining habitat for fishes was essential for the persistence of fishes, and thus, fishery success. These two management strategies prioritised in combination stand to contribute more than the sum of their parts. By targeting management strategies on land to reduce runoff of sediments and nutrients onto coastal coral reefs, while strategically placing new NTMRs in areas less prone to runoff and typhoon exposure, would enhance the benefit of NTMRs greatly. While the challenge is real, with lack of political will and infrastructure and financial limitations often standing in the way of effective and proactive management, there is an increasing receptiveness of managers to integrate management strategies. Overall, the results of this thesis contribute to a solid foundation of critical literature on the interaction of coral reefs within a natural and anthropogenically influenced environment, while presenting many promising avenues for future exploration. Finally, and potentially the most important

future direction of this research, will be to communicate the key findings of this thesis with managers and communities in the Philippines that stand to benefit most.

References

Abesamis, R.A. and Russ, G.R., 2005. Density-dependent spill-over from a marine reserve: Long-term evidence. Ecological Applications, 15(5), pp.1798-1812.

Abesamis, R.A., Russ, G.R. and Alcala, A.C., 2006. Gradients of abundance of fish across no-take marine reserve boundaries: evidence from Philippine coral reefs. Aquatic Conservation: Marine and Freshwater Ecosystems, 16(4), pp.349-371.

Abesamis, R.A., Green, A.L., Russ, G.R. and Jadloc, C.R.L., 2014. The intrinsic vulnerability to fishing of coral reef fishes and their differential recovery in fishery closures. Reviews in Fish Biology and Fisheries, 24(4), pp.1033-1063.

Abesamis, R.A., Jadloc, C.R.L. and Russ, G.R., 2015. Varying annual patterns of reproduction in four species of coral reef fish in a monsoonal environment. Marine Biology, 162(10), pp.1993-2006.

Abesamis, R.A., Saenz-Agudelo, P., Berumen, M.L., Bode, M., Jadloc, C.R.L., Solera, L.A., Villanoy, C.L., Bernardo, L.P.C., Alcala, A.C. and Russ, G.R., 2017. Reef-fish larval dispersal patterns validate no-take marine reserve network connectivity that links human communities. Coral Reefs, 36(3), pp.791-801.

Adam, T.C., Schmitt, R.J., Holbrook, S.J., Brooks, A.J., Edmunds, P.J., Carpenter, R.C. and Bernardi, G., 2011. Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. PLoS One, 6(8), p.e23717.

Adam, T.C., Brooks, A.J., Holbrook, S.J., Schmitt, R.J., Washburn, L. and Bernardi, G., 2014. How will coral reef fish communities respond to climate-driven disturbances? Insight from landscape-scale perturbations. Oecologia, 176(1), pp.285-296.

Alcala, A.C., and Russ, G.R., 2002. Status of Philippine coral reef fisheries. Asian Fisheries Science, 15, pp.177-192.

Alcala, A. C., and Russ, G. R., 2006. No-take marine reserves and reef fisheries management in the Philippines: a new people power revolution. AMBIO: A Journal of the Human Environment, 35(5), pp.245-254.

Alcala, A.C., Bucol, A.A., and Nillos-Kleiven, P., 2008. Directory of Marine Reserves in the Visayas, Philippines. Foundation for the Philippine Environment and Silliman University-Angelo King Center for Research and Environmental Management (SUAKCREM). Dumaguete, Philippines.

Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications, 8:79–92.

Almany, G. R., Berumen, M. L., Thorrold, S. R., Planes, S., and Jones, G. P., 2007. Local replenishment of coral reef fish populations in a marine reserve. Science, 316(5825), pp.742-744.

Almany, G.R., Connolly, S.R., Heath, D.D., Hogan, J.D., Jones, G.P., McCook, L.J., Mills, M., Pressey, R.L. and Williamson, D.H., 2009. Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs, 28(2), pp.339-351.

Almany, G.R., Hamilton, R.J., Bode, M., Matawai, M., Potuku, T., Saenz-Agudelo, P., Planes, S., Berumen, M.L., Rhodes, K.L., Thorrold, S.R. and Russ, G.R., 2013. Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. Current Biology, 23(7), pp.626-630.

Alquezar, R., Glendenning, L. and Costanzo, S., 2013. The use of the brown macroalgae, Sargassum flavicans, as a potential bioindicator of industrial nutrient enrichment. Marine Pollution Bulletin, 77(1-2), pp.140-146.

Alvarez-Romero, J.G., Pressey, R.L., Ban, N.C., Vance-Borland, K., Willer, C., Klein, C.J. and Gaines, S.D., 2011. Integrated land-sea conservation planning: the missing links. Annual Review of Ecology, Evolution, and Systematics, 42.

Anderson, M., Gorley, R.N., and Clarke, R.K., 2008. Permanova+ for Primer: Guide to Software and Statistical Methods. Primer-E Limited. https://doi.org/10.13564/j.cnki.issn.1672-9382.2013.01.010

Andrews, J., and Gentien, P. 1982. Upwelling as a source of nutrients for the Great Barrier Reef Ecosystems: A solution to Darwin's question? Marine Ecology Progress Series, 8, pp.257–269. https://doi.org/10.3354/meps008257

Ateweberhan, M., Bruggemann, J.H. and Breeman, A.M., 2005. Seasonal dynamics of Sargassum ilicifolium (Phaeophyta) on a shallow reef flat in the southern Red Sea (Eritrea). Marine Ecology Progress Series, 292, pp.159-171.

Babcock, R. and Smith, L., 2002, January. Effects of sedimentation on coral settlement and survivorship. In Proceedings of the Ninth International Coral Reef Symposium, Bali, 23-27 October 2000, Vol. 1, pp.245-248.

Babcock, R.C., Shears, N.T., Alcala, A.C., Barrett, N.S., Edgar, G.J., Lafferty, K.D., McClanahan, T.R. and Russ, G.R., 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proceedings of the National Academy of Sciences, 107(43), pp.18256-18261.

Babcock, R.C., Dambacher, J.M., Morello, E.B., Plagányi, É.E., Hayes, K.R., Sweatman, H.P. and Pratchett, M.S., 2016. Assessing different causes of crown-of-thorns starfish outbreaks and appropriate responses for management on the Great Barrier Reef. PloS One, 11(12), p.e0169048.

Balmford, A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, R.E., Jenkins, M., Jefferiss, P., Jessamy, V., Madden, J. and Munro, K., 2002. Economic reasons for

conserving wild nature. science, 297(5583), pp.950-953. https://doi.org/10.1126/science.1073947

Bauman, A.G., Hoey, A.S., Dunshea, G., Feary, D.A., Low, J., and Todd, P.A., 2017. Macroalgal browsing on a heavily degraded, urbanized equatorial reef system. Scientific Reports, 7(1), p.8352.

Bellwood, D. R., and Wainwright, P., 2001. Locomotion in labrid fishes: Implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. Coral Reefs, 20(2), 139–150. https://doi.org/10.1007/s003380100156

Bellwood, D. R., Hoey, A. S., Ackerman, J. L., and Depczynski, M., 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Global Change Biology, 12(9), pp.1587-1594. https://doi.org/10.1111/j.1365-2486.2006.01204.x

Bellwood, D.R. and Fulton, C.J., 2008. Sediment-mediated suppression of herbivory on coral reefs: Decreasing resilience to rising sea-levels and climate change?. Limnology and Oceanography, 53(6), pp.2695-2701.

Bellwood, D. R., Baird, A. H., Depczynski, M., González-Cabello, A., Hoey, A. S., Lefèvre, C. D., and Tanner, J. K. 2012. Coral recovery may not herald the return of fishes on damaged coral reefs. Oecologia, 170(2), pp.567–573. https://doi.org/10.1007/s00442-012-2306-z

Bellwood, D.R., Tebbett, S.B., Bellwood, O., Mihalitsis, M., Morais, R.A., Streit, R.P. and Fulton, C.J., 2018. The role of the reef flat in coral reef trophodynamics: Past, present, and future. Ecology and Evolution, 8(8), pp.4108-4119.

Bellwood, D.R., Streit, R.P., Brandl, S J., and Tebbett, S.B., 2019. The meaning of the term “function” in ecology: a coral reef perspective. Functional Ecology, 0–1. https://doi.org/10.1111/1365-2435.13265

Bergseth, B.J., Russ, G.R. and Cinner, J.E., 2015. Measuring and monitoring compliance in no-take marine reserves. Fish and Fisheries, 16(2), pp.240-258.

Berkes, F., 2001. Managing small-scale fisheries: alternative directions and methods. IDRC.

Blake, J.G., and Loiselle, B.A., 2017. Diversity of birds along an elevational gradient in the Cordillera Central , Costa Rica, 117(3), pp.663–686.

Botsford, L.W., White, J.W., Coffroth, M.A., Paris, C.B., Planes, S., Shearer, T.L., Thorrold, S.R. and Jones, G.P., 2009. Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. Coral reefs, 28(2), pp.327-337.

Boyce, D.G., Frank, K.T., Worm, B. and Leggett, W.C., 2015. Spatial patterns and predictors of trophic control in marine ecosystems. Ecology Letters, 18(10), pp.1001-1011.

Brawley, S.H. and Adey, W.H., 1981. The effect of micrograzers on algal community structure in a coral reef microcosm. Marine Biology, 61(2-3), pp.167-177.

Brierley, A.S. and Kingsford, M.J., 2009. Impacts of climate change on marine organisms and ecosystems. Current Biology, 19(14), R602-R614.

Bruno, J.F., Côté, I.M., and Toth, L.T., 2019. Climate change, coral loss, and the curious case of the parrotfish paradigm: Why don't marine protected areas improve reef resilience? Annual Review of Marine Science, 11, pp.307-34.

Butcher, J.G., 2004. The closing of the frontier: A history of the marine fisheries of Southeast Asia, c.1850-2000 (No. 8). Institute of Southeast Asian Studies.

Cabral, R.B., and Geronimo, R.C., 2018. How important are coral reefs to food security in the Philippines? Diving deeper than national aggregates and averages. Marine Policy. 91, pp.136-141.

Campbell, S.J., Hoey, A.S., Maynard, J., Kartawijaya, T., Cinner, J., Graham, N.A. and Baird, A.H., 2012. Weak compliance undermines the success of no-take zones in a large government-controlled marine protected area. PloS one, 7(11), p.e50074.

Carassou, L., Kulbicki, M., Nicola, T.J. and Polunin, N.V., 2008. Assessment of fish trophic status and relationships by stable isotope data in the coral reef lagoon of New Caledonia, southwest Pacific. Aquatic Living Resources, 21(1), pp.1-12.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A. and Kinzig, A.P., 2012. Biodiversity loss and its impact on humanity. Nature, 486(7401), p.59.

Casey, J.M., Baird, A.H., Brandl, S.J., Hoogenboom, M.O., Rizzari, J.R., Frisch, A.J., Mirbach, C.E., Connolly, S.R., 2016. A test of trophic cascade theory: fish and benthic assemblages across a predator density gradient on coral reefs. Oecologia, 183(1), pp.1-15.

Cheal A.J., Wilson S.K., Emslie M.J., Dolman A. and Sweatman H.P.A., 2008. Responses of reef fish communities to coral declines on the Great Barrier Reef. Marine Ecology Progress Series, 372, pp.211-223.

Cheal, A., Emslie, M., Miller, I., and Sweatman, H., 2012. The distribution of herbivorous fishes on the Great Barrier Reef. Marine Biology, 159, pp.1143–1154. https://doi.org/10.1007/s00227-012-1893-x

Cheal, A.J., Emslie, M., MacNeil, M.A., Miller, I. and Sweatman, H., 2013. Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs. Ecological Applications, 23(1), pp.174-188.

Choat, J.H. and Axe, L.M., 1996. Growth and longevity in acanthurid fishes; an analysis of otolith increments. Marine Ecology Progress Series, 134, pp.15-26.

Choat, J.H. and Axe, L.M., 1996. Growth and longevity in acanthurid fishes; an analysis of otolith increments. Marine Ecology Progress Series, 134, pp.15-26.

Choat, J., Clements, K. and Robbins, W., 2002. The trophic status of herbivorous fishes on coral reefs. Marine Biology, 140(3), pp.613-623. https://doi.org/10.1007/s00227-001-0715-3

Christie, M.R., Tissot, B.N., Albins, M.A., Beets, J.P., Jia, Y., Ortiz, D.M., Thompson, S.E. and Hixon, M.A., 2010. Larval connectivity in an effective network of marine protected areas. PloS one, 5(12), p.e15715.

Cinner, J.E., Graham, N.A., Huchery, C., and MacNeil, M.A., 2013. Global effects of local human population density and distance to markets on the condition of coral reef fisheries. Conservation Biology. 27(3), pp.453-458.

Cinner, J.E., Maire, E., Huchery, C., MacNeil, M.A., Graham, N.A., Mora, C., McClanahan, T.R., Barnes, M.L., Kittinger, J.N., Hicks, C.C. and D'agata, S., 2018. Gravity of human impacts mediates coral reef conservation gains. Proceedings of the National Academy of Sciences, 115(27), pp.E6116-E6125.

Clarke, K., and Warwick, R. 2001. Change in marine communities: An approach to statistical analysis and interpretation (2nd ed.). Plymouth, UK: PRIMER-E, Ltd. Plymouth Marine Laboratory.

Clements, C.S., Rasher, D.B., Hoey, A.S., Bonito, V.E., and Hay, M.E. 2018. Spatial and temporal limits of coral-macroalgal competition: The negative impacts of macroalgal density, proximity, and history of contact. Marine Ecology Progress Series, 586, pp.11–20. https://doi.org/10.3354/meps12410

Clements, K.D. and Choat, J.H. 1993. Marine Biology. Influence of season, ontogeny and tide on the diet of the temperate marine herbivorous fish Odax pullus (Odacidae), 117, p.213. https://doi.org/10.1007/BF00345665

Clements, K.D., German, D.P., Piché, J., Tribollet, A., and Choat, J.H., 2016. Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. Biological Journal of the Linnean Society. 120(4), pp.729-751. https://doi.org/10.1111/bij.12914

Coker, D.J., Wilson, S.K., & Pratchett, M.S., 2014. Importance of live coral habitat for reef fishes. Reviews in Fish Biology and Fisheries, 24(1), pp.89-126.

Comeros-Raynal, M.T., Choat, J.H., Polidoro, B.A., Clements, K.D., Abesamis, R., Craig, M.T., Lazuardi, M.E., McIlwain, J., Muljadi, A., Myers, R.F. and Nañola Jr, C.L., 2012. The likelihood of extinction of iconic and dominant herbivores and detritivores of coral reefs: the parrotfishes and surgeonfishes. PLoS One, 7(7), p.e39825.

Costalago, D., Navarro, J., Álvarez-Calleja, I. and Palomera, I., 2012. Ontogenetic and seasonal changes in the feeding habits and trophic levels of two small pelagic fish species. Marine Ecology Progress Series, 460, pp.169-181.

Crossman, D.J., Choat, J.H. and Clements, K.D., 2005. Nutritional ecology of nominally herbivorous fishes on coral reefs. Marine Ecology Progress Series, 296, pp.129-142.

Cvitanovic, C., Wilson, S.K., Fulton, C.J., Almany, G.R., Anderson, P., Babcock, R.C., Ban, N.C., Beeden, R.J., Beger, M., Cinner, J. and Dobbs, K., 2013. Critical research needs for managing coral reef marine protected areas: perspectives of academics and managers. Journal of environmental management, 114, pp.84-91.

da Silva, I.M., Hill, N., Shimadzu, H., Soares, A.M. and Dornelas, M., 2015. Spillover effects of a community-managed marine reserve. PloS one, 10(4), p.e0111774.

Dalton, T.M., 2005. Beyond biogeography: A framework for involving the public in planning of US marine protected areas. Conservation Biology, 19, pp.1392-1401.

Davis, A.M., Pearson, R.G., Brodie, J.E. and Butler, B., 2017. Review and conceptual models of agricultural impacts and water quality in waterways of the Great Barrier Reef catchment area. Marine and Freshwater Research, 68(1), pp.1-19.

De'ath, G., & Fabricius, K., 2010. Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. Ecological Applications, 20(3), pp.840–850.

Denny, C.M., Willis, T.J. and Babcock, R.C., 2004. Rapid recolonisation of snapper Pagrus auratus: Sparidae within an offshore island marine reserve after implementation of no-take status. Marine Ecology Progress Series, 272, pp.183-190.

Di Musciano, M., Carranza, M. L., Frate, L., Di Cecco, V., Di Martino, L., Frattaroli, A. R., and Stanisci, A. 2018. Distribution of plant species and dispersal traits along environmental gradients in central Mediterranean summits. Diversity, 10(3), pp.1–17. https://doi.org/10.3390/d10030058

Dickens, L.C., Goatley, C.H.R., Tanner, J.K., and Bellwood, D.R., 2011. Quantifying relative diver effects in underwater visual censuses. PLoS ONE, 6(4), pp.6–8. https://doi.org/10.1371/journal.pone.0018965

Done, T. J. 1982. Patterns in the distribution of coral communities across the central Great Barrier Reef. Coral Reefs, 1(2), pp.95–107. https://doi.org/10.1007/BF00301691

Done, T.J. and Reichelt, R.E., 1998. Integrated coastal zone and fisheries ecosystem management: generic goals and performance indices. Ecological Applications, 8(sp1), pp.S110-S118.

Duarte, L.O., and Garcıa, C.B., 2004. Trophic role of small pelagic fishes in a tropical upwelling ecosystem. Ecological Modelling. 172(2-4), pp.323-338.

Edgar, G.J., Bustamante, R.H., Farina, J.M., Calvopina, M., Martinez, C., and Toral-Granda, M.V., 2004. Bias in evaluating the effects of marine protected areas: the importance of baseline data for the Galapagos Marine Reserve. Environmental Conservation. 31, pp.212-218.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T., Berkhout, J. and Buxton, C.D., 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature, 506(7487), p.216.

Elith, J., Leathwick, J.R. and Hastie, T., 2008. A working guide to boosted regression trees. Journal of Animal Ecology, 77(4), pp.802-813.

Elmhagen, B., and S. P. Rushton. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecology Letters, 10, pp.197–206

Emslie, M.J., Pratchett, M.S., Cheal, A.J., & Osborne, K., 2010. Great Barrier Reef butterflyfish community structure: The role of shelf position and benthic community type. Coral Reefs, 29(3), 705–715. https://doi.org/10.1007/s00338-010-0619-0

Emslie, M.J., Logan, M., Ceccarelli, D.M., Cheal, A. J., Hoey, A.S., Miller, I., and Sweatman, H.P.A., 2012. Regional-scale variation in the distribution and abundance of farming damselfishes on Australia's Great Barrier Reef. Marine Biology. https://doi.org/10.1007/s00227-012-1910-0

Emslie, M.J., Logan, M., Williamson, D.H., Ayling, A.M., MacNeil, M.A., Ceccarelli, D., Cheal, A.J., Evans, R.D., Johns, K.A., Jonker, M.J. and Miller, I.R., 2015. Expectations and outcomes of reserve network performance following re-zoning of the Great Barrier Reef Marine Park. Current Biology, 25(8), pp.983-992.

Engelen, A. H., Breeman, A. M., Olsen, J. L., Stam, W. T., & Åberg, P. (2005). Life history flexibility allows Sargassum polyceratium to persist in different environments subjected to stochastic disturbance events. Coral Reefs, 24(4), pp.670–680. https://doi.org/10.1007/s00338-005-0052-y

Fabricius, K. E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine pollution bulletin, 50(2), pp.125-146.

Fabricius, K., De'ath, G., McCook, L., Turak, E. and Williams, D.M., 2005. Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Marine Pollution Bulletin, 51(1-4), pp.384-398. https://doi.org/10.1016/j.marpolbul.2004.10.041

Feary, D.A., Bauman, A.G., Guest, J. and Hoey, A.S., 2018. Trophic plasticity in an obligate corallivorous butterflyfish. Marine Ecology Progress Series, 605, pp.165-171.

Fletcher, S., Saunders, J. and Herbert, R.J.H., 2011. A review of the ecosystem services provided by broad-scale marine habitats in England's MPA network. Journal of Coastal Research, SI 64 (Proceedings of the 11th International Coastal Symposium), pp.378–383. Szczecin, Poland, ISSN 0749-0208

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., and Holling, C. S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology Evolution and Systematics, pp.557-581. https://doi.org/10.1146/annurev.ecolsys.35.021103.105711

Fox, R.J., Sunderland, T.L., Hoey, A.S., Bellwood, D.R., 2009. Estimating functional roles in coral reef ecosystems: behaviour drives contrasting roles in herbivorous fishes (F: Siganidae). Marine Ecological Progress Series, 385, pp.261–269

Frisch, A. J., Baker, R., Hobbs, J. P. A., & Nankervis, L., 2008. A quantitative comparison of recreational spearfishing and linefishing on the Great Barrier Reef: Implications for management of multi-sector coral reef fisheries. Coral Reefs, 27(1), 85–95. https://doi.org/10.1007/s00338-007-0293-z

Froese, R., and Pauly, D. Fishbase. World Wide Web Electronic Publication. Available online: www.fishbase.org (accessed on 11 November 2018). https://doi.org/10.1061/(ASCE)CO.1943-7862.0000676

Fry, B., 2006. Stable isotope ecology (Vol. 521). New York: Springer.

Fu, C., Hua, X., Li, J., Chang, Z., Pu, Z., & Chen, J., 2006. Elevation patterns of frog species richness and endemic richness in Hengduan Mountains, China: geometric constrains, area and climate effects. Ecography, 29, pp.919–927.

Fulton, C.J., Depczynski, M., Holmes, T.H., Noble, M.M., Radford, B., Wernberg, T. and Wilson, S.K., 2014. Sea temperature shapes seasonal fluctuations in seaweed biomass within the Ningaloo coral reef ecosystem. Limnology and Oceanography, 59(1), pp.156-166.

Gaines, S.D., White, C., Carr, M.H. and Palumbi, S.R., 2010. Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences, 107(43), pp.18286-18293.

Gardner, W.D., 1985. The effect of tilt on sediment trap efficiency. Deep Sea Research Part A. Oceanographic Research Papers, 32(3), pp.349-361.

Gilmour, J.P., Smith, L.D., Heyward, A.J., Baird, A.H., and Pratchett, M.S., 2013. Recovery of an isolated coral reef system following severe disturbance. Science, 340(6128), pp.69–71. https://doi.org/10.1126/science.1232310

Gordon, T.A., Harding, H.R., Wong, K.E., Merchant, N.D., Meekan, M.G., McCormick, M.I., Radford, A.N. and Simpson, S.D., 2018. Habitat degradation negatively

affects auditory settlement behavior of coral reef fishes. Proceedings of the National Academy of Sciences, 115(20), pp.5193-5198. https://doi.org/10.1073/pnas.1719291115

Graham, N.A., Jennings, S., MacNeil, M.A., Mouillot, D. and Wilson, S.K., 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature, 518(7537), pp.94-97.

Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Bijoux, J.P., and Robinson, J., 2006. Dynamic fragility of oceanic coral reef ecosystems. Proceedings of the National Academy of Science USA, 103, pp.8425–8429.

Green, A.L. and Bellwood, D.R. eds., 2009. Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience: a practical guide for coral reef managers in the Asia Pacific region (No. 7). IUCN.

Green, A.L., Fernandes, L., Almany, G., Abesamis, R., McLeod, E., Aliño, P.M., White, A.T., Salm, R., Tanzer, J. and Pressey, R.L., 2014. Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. Coastal Management, 42(2), pp.143-159.

Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A., Gleason, M.G., Mumby, P.J. and White, A.T., 2015. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biological Reviews, 90(4), pp.1215-1247.

Gruner, D.S., 2004. Attenuation of top-down and bottom-up forces in a complex terrestrial community. Ecology, 85(11), pp.3010-3022.

Gunderson, L. H., & Pritchard, L. (Eds.), 2012. Resilience and the behavior of large-scale systems (Vol. 60). Island Press.

Gust, N., Choat, J.H., and Ackerman, J.L., 2002. Demographic plasticity in tropical reef fishes. Marine Biology, 140(5), pp.1039–1051. https://doi.org/10.1007/s00227-001-0773-6

Hall, A.E., Vitale, L. and Kingsford, M.J., 2019. Planktonic larval duration, early growth, and the influence of dietary input on the otolith microstructure of Scolopsis bilineatus (Nemipteridae). Environmental Biology of Fishes, pp.1-12.

Halpern, B.S., Selkoe, K.A., White, C., Albert, S., Aswani, S. and Lauer, M., 2013. Marine protected areas and resilience to sedimentation in the Solomon Islands. Coral Reefs, 32(1), pp.61-69.

Hamilton, R.J., Almany, G.R., Brown, C.J., Pita, J., Peterson, N.A. and Choat, J.H., 2017. Logging degrades nursery habitat for an iconic coral reef fish. Biological Conservation, 210, pp.273-280. https://doi.org/10.1016/j.biocon.2017.04.024

Hamilton, S. L., Caselle, J. E., Malone, D. P., & Carr, M. H., 2010. Incorporating biogeography into evaluations of the Channel Islands marine reserve network. Proceedings of the National Academy of Sciences, 107(43), pp.18272-18277.

Hamner, W.M., Jones, M.S., Carleton, J.H., Hauri, I.R., and Williams, D.M., 1988. Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. Bulletin of Marine Science. 42(3), pp.459-479.

Hanley, T.C. and La Pierre, K.J. eds., 2015. Trophic Ecology: Bottom-Up and Top-Down Interactions across Aquatic and Terrestrial Systems. Cambridge University Press.

Harborne, A.R., Green, A.L., Peterson, N.A., Beger, M., Golbuu, Y., Houk, P., Spalding, M.D., Taylor, B.M., Terk, E., Treml, E.A. and Victor, S., 2018. Modelling and mapping regional-scale patterns of fishing impact and fish stocks to support coral-reef management in Micronesia. Diversity and Distributions, 24(12), pp.1729-1743.

Harrison, H.B., Williamson, D.H., Evans, R.D., Almany, G.R., Thorrold, S.R., Russ, G.R., Feldheim, K.A., Van Herwerden, L., Planes, S., Srinivasan, M. and Berumen, M.L., 2012. Larval export from marine reserves and the recruitment benefit for fish and fisheries. Current biology, 22(11), pp.1023-1028.

Hart, A.M., and Russ, G.R., 1996. Response of herbivorous fishes to crown-of-thorns starfish Acanthaster planci outbreaks. III. Age, growth, mortality and maturity indices of Acanthurus nigrofuscus. Marine Ecology Progress Series, 136(1–3), 25–35. https://doi.org/10.3354/meps136025

Hatcher, B.G., 1988. Coral reef primary productivity: A beggar's banquet. Trends in Ecology and Evolution, 3(5), pp.106–111. https://doi.org/10.1016/0169-5347(88)90117-6

Heenan, A., Hoey, A.S., Williams, G.J. and Williams, I.D., 2016. Natural bounds on herbivorous coral reef fishes. Proceedings of the Royal Society B: Biological Sciences, 283(1843), p.20161716.

Heller, N.E. and Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biological Conservation, 142(1), pp.14-32.

Hempson, T.N., Graham, N.A., MacNeil, M.A., Williamson, D.H., Jones, G.P. and Almany, G.R., 2017. Coral reef mesopredators switch prey, shortening food chains, in response to habitat degradation. Ecology and evolution, 7(8), pp.2626-2635.

Hempson, T.N., Graham, N.A., MacNeil, M.A., Bodin, N. and Wilson, S.K., 2018. Regime shifts shorten food chains for mesopredators with potential sublethal effects. Functional ecology, 32(3), pp.820-830.

Hodgson, G. and Dixon, J.A., 1988. Logging versus fisheries and tourism in Palawan: An environmental and economic analysis. Occasional Papers of the East-West Environment and Policy Institute, 7, pp.1-112.

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K. and Knowlton, N., 2007. Coral reefs under rapid climate change and ocean acidification. science, 318(5857), pp.1737-1742.

Hoegh-Guldberg, O., Hoegh-Guldberg, H., Veron, J.E.N., Green, A., Gomez, E. D., Lough, J., King, M., Ambariyanto, Hansen, L., Cinner, J., Dews, G., Russ, G., Schuttenberg, H. Z., Peñaflor, E.L., Eakin, C. M., Christensen, T. R. L., Abbey, M., Areki, F., Kosaka, R. A., Tewfik, A., Oliver, J. (2010). The Coral Triangle and Climate Change: Ecosystems, People and Societies at Risk. World Wildlife Fund Australia, Brisbane, 276 pp.

Hoey, A.S., and Bellwood, D.R. 2008. Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. Coral Reefs, 27(1), pp.37–47. https://doi.org/10.1007/s00338-007-0287-x

Hoey, A.S., and Bellwood, D.R. 2010. Cross-shelf variation in browsing intensity on the Great Barrier Reef. Coral Reefs, 29(2), pp.499–508. https://doi.org/10.1007/s00338-010-0605-6

Hoey, A.S., Pratchett, M.S., and Cvitanovic, C. 2011. High macroalgal cover and low coral recruitment undermines the potential resilience of the world's southernmost coral reef assemblages. PLoS ONE, 6(10), pp.1–9. https://doi.org/10.1371/journal.pone.0025824

Hoey, A. S., Brandl, S. J., & Bellwood, D. R. 2013. Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: Implications for

ecosystem function. Coral Reefs, 32(4), pp.973–984. https://doi.org/10.1007/s00338-013-1043-z

Hoey, A., Howells, E., Johansen, J., Hobbs, J.P., Messmer, V., McCowan, D., Wilson, S. and Pratchett, M., 2016. Recent advances in understanding the effects of climate change on coral reefs. Diversity, 8(2), p.12. https://doi.org/10.3390/d8020012

Hoey, A. S., & Bonaldo, R. R. (Eds.). 2018. Biology of Parrotfishes. CRC Press.

Holmlund, C.M. and Hammer, M., 1999. Ecosystem services generated by fish populations. Ecological economics, 29(2), pp.253-268.

Horigue, V., Aliño, P.M., White, A.T., and Pressey, R. L. 2012. Marine protected area networks in the Philippines: Trends and challenges for establishment and governance. Ocean & coastal management, 64, pp.15-26.

Horn, M.H. and Neighbors, M.A., 1984. Protein and nitrogen assimilation as a factor in predicting the seasonal macroalgal diet of the monkeyface prickleback. Transactions of the American Fisheries Society, 113(3), pp.388-396.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J. and Lough, J.M., 2003. Climate change, human impacts, and the resilience of coral reefs. Science, 301(5635), pp.929-933.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S. and Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Current Biology, 17(4), pp.360-365.

Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H., Babcock, R.C., Beger, M., Bellwood, D.R., Berkelmans, R. and

Bridge, T.C., 2017. Global warming and recurrent mass bleaching of corals. Nature, 543(7645), p.373.

Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Dietzel, A., Eakin, C.M., Heron, S.F., Hoey, A.S., Hoogenboom, M.O., Liu, G. and McWilliam, M.J., 2018. Global warming transforms coral reef assemblages. Nature, 556(7702), p.492.

Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Chase, T.J., Dietzel, A., Hill, T., Hoey, A.S., Hoogenboom, M.O., Jacobson, M. and Kerswell, A., 2019. Global warming impairs stock–recruitment dynamics of corals. Nature, p.1. http://dx.doi.org/10.1038/s41586-019-1081-y

Huijbers, C.M., Connolly, R.M., Pitt, K.A., Schoeman, D.S., Schlacher, T.A., Burfeind, D.D., Steele, C., Olds, A.D., Maxwell, P.S., Babcock, R.C. and Rissik, D., 2015. Conservation benefits of marine reserves are undiminished near coastal rivers and cities. Conservation Letters, 8(5), pp.312-319.

Hunter, M.D. and Price, P.W., 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology, 73(3), pp.724-732.

Huston, M.A., 1985. Patterns of species diversity on coral reefs. Annual Review of Ecology and Systematics, 16(1), pp.149-177.

Inger, R., Jackson, A., Parnell, A. and Bearhop, S., 2010. SIAR V4 (Stable Isotope Analysis in R). An Ecologist's Guide. Dublin, Ireland.

Jackson, J.B.C, Donovan, M.K., Cramer, K.L. and Lam, V.Y.Y., 2014. Status and Trends of Caribbean Coral Reefs: 1970-2012, Global Coral Reef Monitoring Network (GCRMN). pp. 1-360.

Jennings, S., Reynolds, J.D., Polunin, N.V.C., 1999. Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. Conservation Biology, 13, pp.1466–1475

Johnson, G., Taylor, B., Robbins, W., Franklin, E., Toonen, R., Bowen, B., and Choat, J. 2019. Diversity and Structure of Parrotfish Assemblages across the Northern Great Barrier Reef. Diversity, 11(1), p.14. https://doi.org/10.3390/d11010014

Johnson, J.E. and Welch, D.J., 2009. Marine fisheries management in a changing climate: a review of vulnerability and future options. Reviews in Fisheries Science, 18(1), pp.106-124.

Jones, G.P., McCormick, M.I., Srinivasan, M. and Eagle, J.V., 2004. Coral decline threatens fish biodiversity in marine reserves. Proceedings of the National Academy of Sciences, 101(21), pp.8251-8253.

Khalil, M.T., Bouwmeester, J. and Berumen, M.L., 2017. Spatial variation in coral reef fish and benthic communities in the central Saudi Arabian Red Sea. PeerJ, 5, p.e3410.

Kingsford, M.J., 1989. Distribution patterns of planktivorous reef fish along the coast of northeastern New Zealand. Marine ecology progress series. Oldendorf, 54(1), pp.13-24.

Kiørboe, T., Visser, A., and Andersen, K. H., 2018. A trait-based approach to ocean ecology. ICES Journal of Marine Science, 75, pp.1849–1863. https://doi.org/10.1093/icesjms/fsy090

Knowlton, N., Brainard, R.E., Fisher, R., Moews, M., Plaisance, L. and Caley, M.J., 2010. Coral reef biodiversity. Life in the world's oceans: diversity distribution and abundance, pp.65-74.

Knutson, T.R., McBride, J.L., Chan, J., Emanuel, K., Holland, G., Landsea, C., Held, I., Kossin, J.P., Srivastava, A.K., and Sugi, M., 2010. Tropical cyclones and climate change. Nature Geoscience. 3(3), p.157.

Koop, K., Booth, D., Broadbent, A., Brodie, J., Bucher, D., Capone, D., Coll, J., Dennison, W., Erdmann, M., Harrison, P. and Hoegh-Guldberg, O., 2001. ENCORE: the effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. Marine Pollution Bulletin, 42(2), pp.91-120.

Kronen, M., Magron, F., McArdle, B. and Vunisea, A., 2010. Reef finfishing pressure risk model for Pacific Island countries and territories. Fisheries Research, 101(1-2), pp.1-10.

Kroon, F.J., Schaffelke, B. and Bartley, R., 2014. Informing policy to protect coastal coral reefs: Insight from a global review of reducing agricultural pollution to coastal ecosystems. Marine pollution bulletin, 85(1), pp.33-41.

Kroon, F. J., Thorburn, P., Schaffelke, B. and Whitten, S., 2016. Towards protecting the Great Barrier Reef from land-based pollution. Global Change Biology. doi:10.1111/gcb.13262

Krueck, N.C., Legrand, C., Ahmadia, G.N., Green, A., Jones, G.P., Riginos, C., Treml, E.A. and Mumby, P.J., 2018. Reserve sizes needed to protect coral reef fishes. Conservation Letters, 11(3), p.e12415.

Kulbicki, M., Guillemot, N., Amand, M., 2005. A general approach to length-weight relationships for New Caledonian lagoon fishes. Cybium, 29(3), pp.235-252. https://doi.org/http://dx.doi.org/10.1590/0001-3765201620140532

Lamb, J.B., van de Water, J.A., Bourne, D.G., Altier, C., Hein, M.Y., Fiorenza, E.A., Abu, N., Jompa, J. and Harvell, C.D., 2017. Seagrass ecosystems reduce exposure

to bacterial pathogens of humans, fishes, and invertebrates. Science, 355(6326), pp.731-733.

Lamy, T., Legendre, P., Chancerelle, Y., Siu, G., and Claudet, J., 2015. Understanding the spatio-temporal response of coral reef fish communities to natural disturbances: Insights from beta-diversity decomposition. PLoS ONE, 10(9), pp.1–18. https://doi.org/10.1371/journal.pone.0138696

Largo, B.D. and Ohno, M., 1992. Phenology of two species of brown Seaweeds, Sargassum myriocystum J. Agardh and Sargassum siliquosum J. agardh (sargassaceae, Fucales) in Liloan, Cebu, in Central Philippines.

Leahy, S.M., Russ, G.R. and Abesamis, R.A., 2015a. Primacy of bottom-up effects on a butterflyfish assemblage. Marine and Freshwater Research, 67(8), pp.1175-1185.

Leahy, S. M., Russ, G. R., and Abesamis, R. A., 2015b. Pelagic larval duration and settlement size of a reef fish are spatially consistent, but post-settlement growth varies at the reef scale. Coral Reefs, 34(4), pp.1283-1296.

Ledlie, M.H., Graham, N.A.J., Bythell, J.C., Wilson, S.K., Jennings, S., Polunin, N.V.C., Hardcastle, J., 2007. Phase shifts and the role of herbivory in the resilience of coral reefs. Coral Reefs. 26(3), pp.641-653.

Lefèvre, C.D. and Bellwood, D.R., 2010. Seasonality and dynamics in coral reef macroalgae: variation in condition and susceptibility to herbivory. Marine Biology, 157(5), pp.955-965.

Legendre, P., & Legendre, L. 1998. Numerical ecology: Second English edition. Developments in Environmental Modelling (20th ed.). Amsterdam, the Netherlands: Elsevier.

Leroux, S., and Loreau, M. 2015. Theoretical perspectives on bottom-up and top-down interactions across ecosystems. In T. Hanley & K. La Pierre (Eds.), Trophic

Ecology: Bottom-Up and Top-Down Interactions across Aquatic and Terrestrial Systems (Ecological Reviews, pp. 3-28). Cambridge: Cambridge University Press. doi:10.1017/CBO9781139924856.002

Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airamé, S. and Warner, R.R., 2009. Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series, 384, pp.33-46.

Loffler, Z., Graba-Landry, A., Kidgell, J. T., McClure, E. C., Pratchett, M. S., & Hoey, A. S. (2018). Holdfasts of Sargassum swartzii are resistant to herbivory and resilient to damage. Coral Reefs, 37(4), pp.1075–1084. https://doi.org/10.1007/s00338-018-01745-w

Lubchenco, J., Palumbi, S.R., Gaines, S.D. and Andelman, S., 2003. Plugging a hole in the ocean: the emerging science of marine reserves 1. Ecological applications, 13(sp1), pp.3-7.

Maire, E., Grenouillet, G., Brosse, S., and Villéger, S. 2015. How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. Global Ecology and Biogeography, 24(6), pp.728–740. https://doi.org/10.1111/geb.12299

Mapstone, B.D., Ayling, A.M., and Choat, J.H., 1998. Habitat, cross shelf and regional patterns in the distributions and abundances of some coral reef organisms on the northern Great Barrier Reef - with comment on the implications for future monitoring. Great Barrier Reef Marine Park Authority, (48), p.71.

Martin-Smith, K.M., 1992 Seasonal variation in tropical benthic Sargassum and associated motile epifauna. Proc 7th Int Coral Reef Symp, Guam, 2, pp.881–886

Matley, J.K., Fisk, A.T., Tobin, A.J., Heupel, M.R. and Simpfendorfer, C.A., 2016. Diet-tissue discrimination factors and turnover of carbon and nitrogen stable isotopes in

tissues of an adult predatory coral reef fish, Plectropomus leopardus. Rapid Communications in Mass Spectrometry, 30(1), pp.29-44.

McClanahan, T.R., and Mangi, S., 2000. Spill-over of exploitable fishes from a marine park and its effect in the adjacent fishery. Ecological Applications, 10, pp.1792–1805.

McClanahan, T.R., Marnane, M.J., Cinner, J.E. and Kiene, W.E., 2006. A comparison of marine protected areas and alternative approaches to coral-reef management. Current Biology, 16(14), pp.1408-1413.

McClanahan, T.R., Graham, N.A.J., MacNeil, M.A. and Cinner, J.E., 2015. Biomass-based targets and the management of multispecies coral reef fisheries. Conservation Biology, 29(2), pp.409-417.

McClelland, J.W., Holl, C.M. and Montoya, J.P., 2003. Relating low δ15N values of zooplankton to N2-fixation in the tropical North Atlantic: insights provided by stable isotope ratios of amino acids. Deep Sea Research Part I: Oceanographic Research Papers, 50(7), pp.849-861.

McClure, E.C., Richardson, L.E., Graba-Landry, A., Loffler, Z., Russ, G.R. and Hoey, A.S., 2019. Cross-Shelf Differences in the Response of Herbivorous Fish Assemblages to Severe Environmental Disturbances. Diversity, 11(2), p.23.

McCook, L.J., 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral reefs, 18(4), pp.357-367.

McCook, L.J., Ayling, T., Cappo, M., Choat, J.H., Evans, R.D., De Freitas, D.M., Heupel, M., Hughes, T.P., Jones, G.P., Mapstone, B. and Marsh, H., 2010. Adaptive management of the Great Barrier Reef: A globally significant

demonstration of the benefits of networks of marine reserves. Proceedings of the National Academy of Sciences, 107(43), pp.18278-18285.

McLeod, E., Salm, R., Green, A. and Almany, J., 2009. Designing marine protected area networks to address the impacts of climate change. Frontiers in Ecology and the Environment, 7(7), pp.362-370.

McQueen, D.J., Post, J.R. and Mills, E.L., 1986. Trophic relationships in fresh-water pelagic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences, 43, pp.1571–1581.

Mei, W. and Xie, S.P., 2016. Intensification of landfalling typhoons over the northwest Pacific since the late 1970s. Nature Geoscience, 9(10), p.753.

Mei, W., Xie, S. P., Primeau, F., McWilliams, J. C., & Pasquero, C., 2015. Northwestern Pacific typhoon intensity controlled by changes in ocean temperatures. Science advances, 1(4), e1500014.

Melbourne-Thomas, J., Johnson, C.R., Alino, P.M., Geronimo, R.C., Villanoy, C.L., and Gurney, G.G. 2011. A multi-scale biophysical model to inform regional management of coral reefs in the western Philippines and South China Sea. Environmental Modelling & Software, 26(1), pp.66-82.

Mellin, C., Aaron MacNeil, M., Cheal, A.J., Emslie, M.J. and Julian Caley, M., 2016. Marine protected areas increase resilience among coral reef communities. Ecology letters, 19(6), pp.629-637.

Mellin, C., Thompson, A., Jonker, M.J. and Emslie, M.J., 2019. Cross-Shelf Variation in Coral Community Response to Disturbance on the Great Barrier Reef. Diversity, 11(3), p.38.

Menge, B., and Sutherland, J. 1976. Species Diversity Gradients: Synthesis of the Roles of Predation, Competition, and Temporal Heterogeneity. The American Naturalist, 110(973), pp.351-369.

Mill, A.C., Pinnegar, J.K. and Polunin, N.V.C., 2007. Explaining isotope trophic-step fractionation: why herbivorous fish are different. Functional Ecology, 21(6), pp.1137-1145.

Mora, C., Chittaro, P.M., Sale, P.F., Kritzer, J.P. and Ludsin, S.A., 2003. Patterns and processes in reef fish diversity. Nature, 421(6926), p.933.

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., and Bellwood, D. R. 2013. A functional approach reveals community responses to disturbances. Trends in Ecology and Evolution, 28(3), pp.167–177. https://doi.org/10.1016/j.tree.2012.10.004

Mumby, P. J., Dahlgren, C. P., Harborne, A. R., Kappel, C. V., Micheli, F., Brumbaugh, D. R., … Gill, A. B. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science, 311(5757), pp.98–101. https://doi.org/10.1126/science.1121129

Mumby, P.J., Wolff, N.H., Bozec, Y-M., Chollett, I. and Halloran, P., 2014. Operationalizing the resilience of coral reefs in an era of climate change, Conservation Letters, 7(3), pp.176–187

Munday, P.L., Jones, G.P., Pratchett, M.S. and Williams, A.J., 2008. Climate change and the future for coral reef fishes. Fish and Fisheries, 9(3), pp.261-285.

Nanami A. 2018. Spatial distributions, feeding ecologies, and behavioral interactions of four rabbitfish species (Siganus unimaculatus, S. virgatus, S. corallinus, and S. puellus) PeerJ 6:e6145 https://doi.org/10.7717/peerj.6145

Nañola, C. L., Aliño, P. M., & Carpenter, K. E. (2011). Exploitation-related reef fish species richness depletion in the epicenter of marine biodiversity. Environmental Biology of Fishes, 90(4), pp.405-420.

Nash, K.L., Abesamis, R.A., Graham, N.A., McClure, E.C., Moland, E., 2016. Drivers of herbivory on coral reefs: species, habitat and management effects. Marine Ecology Progress Series. 554, pp.129-140.

Naughton-Treves, L., Holland, M.B. and Brandon, K., 2005. The role of protected areas in conserving biodiversity and sustaining local livelihoods. Annu. Rev. Environ. Resour., 30, pp.219-252.

Neves, L.M. Teixeira-Neves, T.P. Pereira-Filho, G.H. Araújo, F.G. 2016, The farther the better: Effects of multiple environmental variables on reef fish assemblages along a distance gradient from river influences. PLoS One, 11, pp.1–2. https://doi.org/10.1371/journal.pone.0166679

Newman, S.J., and Williams, D.M.B. 1996. Variation in reef associated assemblages of the Lutjanidae and Lethrinidae at different distances offshore in the central Great Barrier Reef. Environmental Biology of Fishes, 46(2), pp.123–138. https://doi.org/10.1007/BF00005214

Newman, S.J., Williams, D.M.B., and Russ, G.R. 1997. Patterns of zonation of assemblages of the Lutjanidae, Lethrinidae and Serranidae (Epinephelinae) within and among mid-shelf and outer-shelf reefs in the central Great Barrier Reef. Marine and Freshwater Research, 48(2), pp.119–128. https://doi.org/10.1071/MF96047

Newton, K., Cote, I.M., Pilling, G.M., Jennings, S. and Dulvy, N.K., 2007. Current and future sustainability of island coral reef fisheries. Current Biology, 17(7), pp.655-658.

Ng, J.S., Wai, T.C. and Williams, G.A., 2007. The effects of acidification on the stable isotope signatures of marine algae and molluscs. Marine chemistry, 103(1-2), pp.97-102.

Nyström, M., Folke, C. and Moberg, F., 2000. Coral reef disturbance and resilience in a human-dominated environment. Trends in Ecology & Evolution, 15(10), pp.413-417.

O'Farrell, S., Bearhop, S., McGill, R.A., Dahlgren, C.P., Brumbaugh, D.R. and Mumby, P.J., 2014. Habitat and body size effects on the isotopic niche space of invasive lionfish and endangered Nassau grouper. Ecosphere, 5(10), pp.1-11.

Olds, A.D., Pitt, K.A., Maxwell, P.S., Babcock, R.C., Rissik, D. and Connolly, R.M., 2014. Marine reserves help coastal ecosystems cope with extreme weather. Global change biology, 20(10), pp.3050-3058.

Padin, J.I.M.T., Santos, T.R.N., Sienes, P.M., Utzurrum, J. and Ginzel, F., 2013. Fishes of the Dumaguete public market, Negros Oriental, Philippines. In Federation of Institutions for Marine and Freshwater Sciences (Philippines) 45th Annual Meeting, Cebu City, Philippines.

Parnell, A. and Jackson, A., 2013. siar: Stable Isotope Analysis in R. R package version 4.2. Available from: Available from: http://CRAN. R-project. org/package= siar.(23 March 2014).

Parnell, A.C., Inger, R., Bearhop, S. and Jackson, A.L., 2010. Source partitioning using stable isotopes: coping with too much variation. PloS one, 5(3), p.e9672.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. and Torres, F., 1998. Fishing down marine food webs. Science, 279(5352), pp.860-863.

Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens, B.X. and Ward, E.J., 2014. Best practices for use of stable isotope

mixing models in food-web studies. Canadian Journal of Zoology, 92(10), pp.823-835.

Pianka, E. R. (1974). Evolutionary Ecology. New York: Harper & Row.

Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M.L., Hereu, B., Milazzo, M., Zabala, M., d'Anna, G. and Pipitone, C., 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environmental Conservation, 27(2), pp.179-200.

Plass-Johnson, J.G., McQuaid, C.D. and Hill, J.M., 2013. Stable isotope analysis indicates a lack of inter-and intra-specific dietary redundancy among ecologically important coral reef fishes. Coral Reefs, 32(2), pp.429-440.

Plass-Johnson, J.G., Ferse, S.C.A., Jompa, J., Wild, C. and Teichberg, M., 2015. Fish herbivory as a key ecological function in a heavily degraded coral reef system. Limnology Oceanography, 60, pp.1382–1391.

Polunin, N.V.C. and Roberts, C.M., 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series, 100, pp.167-167.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology, 83(3), pp.703-718.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J. and Montana, C.G., 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia, 152(1), pp.179-189.

Pratchett, M.S., Munday, P., Wilson, S.K., Graham, N.A., Cinner, J.E., Bellwood, D.R., Jones, G.P., Polunin, N.V. and McClanahan, T.R., 2008. Effects of climate-induced coral bleaching on coral-reef fishes. Ecological and economic

consequences. Oceanography and Marine Biology: Annual Review, 46, pp.251-296.

Pratchett, M.S., Hoey, A.S., Wilson, S.K., Messmer, V. and Graham, N.A., 2011. Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. Diversity, 3(3), pp.424-452. https://doi.org/10.3390/d3030424

Pratchett, M.S., Hoey, A.S., and Wilson, S.K., 2014. Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. Current Opinion in Environmental Sustainability, 7, pp.37-43. https://doi.org/10.1016/j.cosust.2013.11.022

R Development Core Team, and R Core Team. 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://doi.org/10.1007/978-3-540-74686-7

Randall, J.E., 1986. Acanthuridae. p. 811-823. In M.M. Smith and P.C. Heemstra (eds.) Smiths' sea fishes. Springer-Verlag, Berlin.

Randall, J.E., G.R. Allen and R.C. Steene, 1990. Fishes of the Great Barrier Reef and Coral Sea. University of Hawaii Press, Honolulu, Hawaii. 506 p.

Rasher, D.B., Hoey, A.S. and Hay, M.E., 2013. Consumer diversity interacts with prey defences to drive ecosystem function. Ecology, 94(6), pp.1347-1358.

Reaka-Kudla, M.L., 1997. The global biodiversity of coral reefs: a comparison with rain forests. Biodiversity II: Understanding and protecting our biological resources, 2, p.551.

Richardson, L.E., Graham, N.A., Pratchett, M.S., Eurich, J.G., Hoey, A.S., 2018. Mass coral bleaching causes biotic homogenization of reef fish assemblages. Global Change Biology, 24(7), pp.3117-3129. DOI:10.1111/gcb.14119

Ricklefs, R.E., 1987. Community diversity: relative roles of local and regional processes. Science, 235(4785), pp.167-171.

Rizzari, J.R., Bergseth, B.J., and Frisch, A.J. 2015. Impact of conservation areas on trophic interactions between apex predators and herbivores on coral reefs. Conservation Biology: The Journal of the Society for Conservation Biology, 29(2), pp.418–429. https://doi.org/10.1111/cobi.12385

Roberts, C.M., 1995. Effects of fishing on the ecosystem structure of coral reefs. Conservation Biology. 9(5), pp.988-995.

Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P. and Goodridge, R., 2001. Effects of marine reserves on adjacent fisheries. Science, 294(5548), pp.1920-1923.

Roberts, C.M., O'Leary, B.C., McCauley, D.J., Cury, P.M., Duarte, C.M., Lubchenco, J., Pauly, D., Sáenz-Arroyo, A., Sumaila, U.R., Wilson, R.W. and Worm, B., 2017. Marine reserves can mitigate and promote adaptation to climate change. Proceedings of the National Academy of Sciences, 114(24), pp.6167-6175.

Rogers, C. S., 1990. Responses of coral reefs and reef organisms to sedimentation. Marine Ecology Progress Series. Oldendorf, 62(1), pp.185-202.

Russ, G. 1984. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. Marine Ecology Progress Series, 20, pp.23–34. https://doi.org/10.3354/meps020023

Russ, G.R., 1984. The distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Levels of variability across the entire continental shelf. Marine Ecology Progress Series, 20, pp.23–34

Russ, G.R., Alcala, A.C., 1998. Natural fishing experiments in marine reserves 1983–1993: roles of life history and fishing intensity in family responses. Coral Reefs, 17(4), pp.399-416.

Russ, G.R. and McCook, L.J., 1999. Potential effects of a cyclone on benthic algal production and yield to grazers on coral reefs across the central Great Barrier Reef. Journal of Experimental Marine Biology and Ecology, 235(2), pp.237-254.

Russ, G.R., 2003. Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. Coral Reefs, 22(1), pp.63-67.

Russ, G. R., Alcala, A. C., and Maypa, A. P., 2003. Spillover from marine reserves: the case of Naso vlamingii at Apo Island, the Philippines. Marine Ecology Progress Series, 264, 15-20.

Russ, G.R., Alcala, A.C., Maypa, A.P., Calumpong, H.P., and White, A.T., 2004. Marine reserve benefits local fisheries. Ecological Applications, 14(2), pp.597-606.

Russ, G.R., and Alcala, A.C., 2011. Enhanced biodiversity beyond marine reserve boundaries: The cup spillith over. Ecological Applications, 21(1), pp.241-250.

Russ, G.R., Miller, K.I., Rizzari, J.R. and Alcala, A.C., 2015a. Long-term no-take marine reserve and benthic habitat effects on coral reef fishes. Marine Ecology Progress Series, 529, pp.233-248.

Russ, G.R., Questel, S.L.A., Rizzari, J.R., and Alcala, A.C. 2015b. The parrotfish–coral relationship: refuting the ubiquity of a prevailing paradigm. Marine Biology, 162(10), pp.2029-2045. https://doi.org/10.1007/s00227-015-2728-3

Russ, G.R. Payne, C.S. Bergseth, B.J. Rizzari, J.R. Abesamis, R.A. and Alcala, A.C. 2018, Decadal-scale response of detritivorous surgeonfishes (family Acanthuridae) to no-take marine reserve protection and changes in benthic habitat. Journal of Fish Biology, 93(5), pp.887–900. https://doi.org/10.1111/jfb.13809

Russ, G.R., Aller-Rojas, O.D., Rizzari, J.R., and Alcala, A.C., 2017. Off-reef planktivorous reef fishes respond positively to decadal-scale no-take marine reserve protection and negatively to benthic habitat change. Marine Ecology, 38(3), e12442.

Russ, G.R., Leahy, S.M., 2017. Rapid decline and decadal-scale recovery of corals and Chaetodon butterflyfish on Philippine coral reefs. Marine Biology, 164(1), p.29

Salvat, B., 1987. Dredging in coral reefs. In: Salvat, B. (ed.) Human impacts on coral reefs: facts and recommendations. Antenne Museum EPHE, Moorea, French Polynesia, pp.165-184

Samoilys, M.A., Martin-Smith, K.M., Giles, B.G., Cabrera, B., Anticamara, J.A., Brunio, E.O. and Vincent, A.C., 2007. Effectiveness of five small Philippines' coral reef reserves for fish populations depends on site-specific factors, particularly enforcement history. Biological conservation, 136(4), pp.584-601.

Samoilys, M., Roche, R., Koldewey, H. and Turner, J., 2018. Patterns in reef fish assemblages: Insights from the Chagos Archipelago. PloS one, 13(1), p.e0191448.

Shears, N.T. and Babcock, R.C., 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia, 132(1), pp.131-142.

Shears, N.T. and Babcock, R.C., 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Marine Ecology Progress Series, 246, pp.1-16.

Shears, N.T., Babcock, R.C. and Salomon, A.K., 2008. Context-dependent effects of fishing: variation in trophic cascades across environmental gradients. Ecological Applications, 18(8), pp.1860-1873.

Smith, J.E., Hunter, C.L. and Smith, C.M. 2010. The effects of top-down vs. bottom-up control on benthic coral reef community structure. Oecologia, 163, p.497. https://doi.org/10.1007/s00442-009-1546-z

Smith, V.H., Tilman, G.D. and Nekola, J.C., 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environmental Pollution, 100(1-3), pp.179-196.

Sotiropoulos, M.A., Tonn, W.M. and Wassenaar, L.I., 2004. Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: potential consequences for food web studies. Ecology of Freshwater Fish, 13(3), pp.155-160.

Stevens, T 2013, Suspended sediment sampler, 2013206318

Stockwell, B., Jadloc, C.R.L., Abesamis, R.A., Alcala, A.C., and Russ, G.R. 2009. Trophic and benthic responses to no-take marine reserve protection in the Philippines. Marine Ecology Progress Series, 389, pp.1-15.

Stoeckl, N., Hicks, C.C., Mills, M., Fabricius, K., Esparon, M., Kroon, F., Kaur, K. and Costanza, R., 2011. The economic value of ecosystem services in the Great Barrier Reef: our state of knowledge. Annals of the New York Academy of Sciences, 1219(1), pp.113-133.

Streit, R.P., Hoey, A.S. and Bellwood, D.R., 2015. Feeding characteristics reveal functional distinctions among browsing herbivorous fishes on coral reefs. Coral Reefs, 34(4), pp.1037-1047. 1037–1047. https://doi.org/10.1007/s00338-015-1322-y

Sweeting, C.J., Barry, J., Barnes, C., Polunin, N.V.C. and Jennings, S., 2007. Effects of body size and environment on diet-tissue δ15N fractionation in fishes. Journal of Experimental Marine Biology and Ecology, 340(1), pp.1-10.

Taylor, B.M., Houk, P., Russ, G.R. and Choat, J.H., 2014. Life histories predict vulnerability to overexploitation in parrotfishes. Coral Reefs, 33(4), pp.869-878.

Taylor BM, Lindfield SJ, Choat JH. 2015. Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. Ecography, 38(5), pp.520-530.

Team, R.C., 2016. R Foundation for Statistical Computing 2016. R: A language and environment for statistical computing. Vienna

Tebbett, S.B., Bellwood, D.R. and Purcell, S.W., 2018. Sediment addition drives declines in algal turf yield to herbivorous coral reef fishes: implications for reefs and reef fisheries. Coral Reefs, 37(3), pp.929-937.

Teh, L.S., Teh, L.C. and Sumaila, U.R., 2013. A global estimate of the number of coral reef fishers. PLoS One, 8(6), p.e65397.

Thiel, R., Sepulveda, A., Kafemann, R., and Nellen, W., 1995. Environmental factors as forces structuring the fish community of the Elbe Estuary. Journal of Fish Biology, 46(1), pp.47–69. https://doi.org/10.1111/j.1095-8649.1995.tb05946.x

Tobey, J., and Torell, E., 2006. Coastal poverty and MPA management in mainland Tanzania and Zanzibar. Ocean & Coastal Management, 49(11), pp.834-854.

Weber, M., De Beer, D., Lott, C., Polerecky, L., Kohls, K., Abed, R.M., Ferdelman, T.G., Fabricius, K.E., 2012. Mechanisms of damage to corals exposed to sedimentation. Proceedings of the National Academy of Sciences. 109(24). E1558-E1567.

Weeks, R., Russ, G.R., Alcala, A.C. and White, A.T., 2010. Effectiveness of marine protected areas in the Philippines for biodiversity conservation. Conservation Biology, 24(2), pp.531-540.

Weeks, R., Baird, M., Amolo, R., Catitig, R., Eisma-Osorio, R.L., Pressey, B. and Alicea, E., 2012. Developing a provincial marine protected area network management for Siquijor, Philippines.

Weeks, R., Aliño, P.M., Atkinson, S., Beldia, P., Binson, A., Campos, W.L., Djohani, R., Green, A.L., Hamilton, R., Horigue, V. and Jumin, R., 2014. Developing marine protected area networks in the Coral Triangle: good practices for expanding the Coral Triangle Marine Protected Area System. Coastal Management, 42(2), pp.183-205.

Weeks, R., Green, A.L., Joseph, E., Peterson, N. and Terk, E., 2017. Using reef fish movement to inform marine reserve design. Journal of Applied Ecology, 54(1), pp.145-152.

Wenger, A.S., Williamson, D.H., da Silva, E.T., Ceccarelli, D.M., Browne, N.K., Petus, C. and Devlin, M.J., 2015. Effects of reduced water quality on coral reefs in and out of no-take marine reserves. Conservation Biology, 30(1), pp.142-153.

Wilkinson, C.C., and Cheshire, A.A., 1988. Cross-shelf variations in coral reef structure and function-influences of land and ocean. Status review. In Proceedings of the 6th International Coral Reef Symposium, Townsville, Australia 8-12 August 1988.

Williams, D. M. 1991. Patterns and processes in the distribution of coral reef fishes. In P. Sale (Ed.), Ecology of Coral Reef Fishes (pp. 437–474). Academic Press.

Williams, D. M., & Hatcher, A. I. 1983. Structure of Fish Communities on Outer Slopes of Inshore, Mid-Shelf and Outer Shelf Reefs of the Great Barrier Reef. Marine Ecology Progress Series, 10, pp.239–250. https://doi.org/10.3354/meps010239

Williams, D.M., Russ, G.G., and Doherty, P.P. 1986. Reef fishes: large-scale distributions, trophic interactions and life cycles. Oceanus, 29, pp.76–82.

Williamson, D.H., Ceccarelli, D.M., Evans, R.D., Jones, G.P. and Russ, G.R., 2014. Habitat dynamics, marine reserve status, and the decline and recovery of coral reef fish communities. Ecology and evolution, 4(4), pp.337-354.

Willis, T.J., Millar, R.B. and Babcock, R.C., 2000. Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. Marine Ecology Progress Series, 198, pp.249-260.

Wilson, S.K., Graham, N.A., Pratchett, M.S., Jones, G.P., Polunin, N.V., 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Global Change Biology. 12(11), pp.2220-2234. https://doi.org/10.1111/j.1365-2486.2006.01252.x

Wilson, S.K., Graham, N.A.J. and Polunin, N.V.C., 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Marine Biology, 151(3), pp.1069-1076.

Wilson, S.K., Burgess, S.C., Cheal, A.J., Emslie, M., Fisher, R., Miller, I., Polunin, N.V. and Sweatman, H.P., 2008. Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. Journal of Animal Ecology, 77(2), pp.220-228.

Wismer, S., Hoey, A.S., and Bellwood, D.R., 2009. Cross-shelf benthic community structure on the Great Barrier Reef: Relationships between macroalgal cover and herbivore biomass. Marine Ecology Progress Series, 376, pp.45–54. https://doi.org/10.3354/meps07790

Wolanski, E., and Hamner, W.M., 1988. Topographically controlled fronts in the ocean and their biological influence. Science. 241(4862), pp.177-181.

Wong, C.M., Conti-Jerpe, I., Raymundo, L.J., DingleWong, C.M., Conti-Jerpe, I., Raymundo, L.J., Dingle, C., Araujo, G., Ponzo, A., and Baker, D.M., 2019. Whale

Shark Tourism: Impacts on Coral Reefs in the Philippines. Environmental Management, 63(2), pp.282-291.

Yambao, A.C., White, A.T., Ablong, W.E. and Alcala, M.R., 2001. Coastal environmental profile of Negros Oriental, Philippines. Coastal Resource Management Project, Cebu City, Philippines.

Yurkowski, D.J., Hussey, N.E., Semeniuk, C., Ferguson, S.H. and Fisk, A.T., 2015. Effects of lipid extraction and the utility of lipid normalization models on δ 13 C and δ 15 N values in Arctic marine mammal tissues. Polar Biology, 38(2), pp.131-143.

Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. Analysing ecological data. In: Gail M, Krickeberg, K., Sarnet, J., Tsiatis, A., Wong, W. (eds) Springer Science and Business Media, LLC

Appendix A. Supplemental information for Chapter 2:

Cross-shelf differences in the response of herbivorous fish assemblages to severe environmental disturbances

Table S2.1. Fish traits assigned to surveyed species. Trait classification based on published literature (Green and Bellwood 2009; Mouillot et al. 2013; Froese and Pauly 2018). Schooling trait categories abbreviated as follows: Small groups (SmallG); medium groups (MedG); large groups (LargeG).

Species	Max body-size (TL cm)	Diet	Mobility	Activity	Social grouping	Position
Acanthurus blochii	51-60	Grazer/detritivore	Mobile within reef	Diurnal	SmallG	Benthic
Acanthurus dussumieri	51-60	Grazer/detritivore	Sedentary	Nocturnal	MedG	Bentho-pelagic
Acanthurus grammoptilus	31-40	Grazer/detritivore	Mobile within reef	Diurnal	SmallG	Bentho-pelagic
Acanthurus lineatus	31-40	Grazer/detritivore	Territorial	Diurnal	Solitary	Bentho-pelagic
Acanthurus nigricans	21-30	Grazer/detritivore	Sedentary	Diurnal	SmallG	Benthic
Acanthurus nigricauda	31-40	Grazer/detritivore	Mobile within reef	Diurnal	SmallG	Benthic
Acanthurus nigrofuscus	21-30	Grazer/detritivore	Sedentary	Diurnal	SmallG	Benthic
Acanthurus olivaceus	31-40	Grazer/detritivore	Mobile within reef	Diurnal	SmallG	Benthic
Acanthurus triostegus	21-30	Grazer/detritivore	Sedentary	Diurnal	Solitary	Bentho-pelagic
Acanthurus xanthopterus	61-70	Grazer/detritivore	Mobile within reef	Diurnal	MedG	Benthic
Bolbometopon muricatum	≥100	Excavator	Mobile across reefs	Diurnal	MedG	Benthic
Calotomus carolinus	51-60	Browser	Mobile within reef	Nocturnal	LargeG	Bentho-pelagic
Cetoscarus ocellatus	71-80	Excavator	Mobile within reef	Diurnal	SmallG	Benthic
Chlorurus japanensis	31-40	Excavator	Mobile within reef	Diurnal	SmallG	Benthic
Chlorurus microrhinos	61-70	Excavator	Mobile within reef	Diurnal	SmallG	Benthic
Chlorurus spilurus	31-40	Excavator	Mobile within reef	Diurnal	SmallG	Benthic
Ctenochaetus binotatus	21-30	Detritivore	Sedentary	Diurnal	Solitary	Benthic
Ctenochaetus striatus	21-30	Detritivore	Sedentary	Diurnal	MedG	Benthic
Hipposcarus longiceps	51-60	Scraper	Mobile within reef	Diurnal	MedG	Benthic
Kyphosus cinerascens	41-50	Browser	Mobile across reefs	Diurnal	MedG	Bentho-pelagic
Kyphosus vaigiensis	61-70	Browser	Mobile across reefs	Diurnal	MedG	Bentho-pelagic
Lo vulpinus	21-30	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Naso annulatus	≥100	Grazer/Planktivore	Sedentary	Nocturnal	Pairing	Pelagic
Naso brachycentron	≥100	Browser	Sedentary	Nocturnal	Pairing	Bentho-pelagic
Naso brevirostris	41-50	Grazer/Planktivore	Mobile across reefs	Diurnal	LargeG	Bentho-pelagic
Naso lituratus	51-60	Browser	Mobile within reef	Diurnal	SmallG	Benthic
Naso tonganus	61-70	Browser	Mobile within reef	Diurnal	SmallG	Benthic
Naso unicornis	71-80	Browser	Mobile within reef	Diurnal	SmallG	Benthic
Naso vlamingii	51-60	Grazer/Planktivore	Mobile across reefs	Diurnal	SmallG	Bentho-pelagic

Platax sp	61-70	Browser	Mobile across reefs	Diurnal	MedG	Bentho-pelagic
Scarus altipinnis	51-60	Scraper	Mobile within reef	Diurnal	LargeG	Benthic
Scarus chameleon	31-40	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus dimidiatus	31-40	Scraper	Mobile within reef	Diurnal	SmallG	Benthic
Scarus flavipectoralis	31-40	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus forsteni	51-60	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus frenatus	41-50	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus ghobban	71-80	Scraper	Mobile within reef	Diurnal	SmallG	Benthic
Scarus globiceps	41-50	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus niger	31-40	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus oviceps	31-40	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Scarus psittacus	31-40	Scraper	Mobile within reef	Diurnal	MedG	Benthic
Scarus rivulatus	31-40	Scraper	Mobile within reef	Diurnal	MedG	Benthic
Scarus rubroviolaceus	61-70	Scraper	Mobile within reef	Nocturnal	MedG	Bentho-pelagic
Scarus schlegeli	31-40	Scraper	Mobile within reef	Diurnal	MedG	Benthic
Scarus sp	41-50	Scraper	Mobile within reef	Diurnal	SmallG	Benthic
Scarus spinus	21-30	Scraper	Mobile within reef	Diurnal	Solitary	Benthic
Siganus argenteus	31-40	Grazer/detritivore	Sedentary	Nocturnal	Solitary	Bentho-pelagic
Siganus canaliculatus	31-40	Browser	Sedentary	Nocturnal	Solitary	Bentho-pelagic
Siganus coralinus	31-40	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus doliatus	31-40	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus puellus	31-40	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus punctatus	31-40	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus sp	31-40	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic
Siganus spinus	21-30	Grazer/detritivore	Mobile across reefs	Diurnal	LargeG	Benthic
Zebrasoma scopas	41-50	Grazer/detritivore	Mobile within reef	Diurnal	SmallG	Benthic
Zebrasoma velifer	41-50	Grazer/detritivore	Mobile within reef	Diurnal	Pairing	Benthic

Table S2.2 Two-way nested PERMANOVA pairwise comparisons with Monte Carlo sampling estimates of taxonomic composition of herbivorous fish among shelf position and between years. Comparisons based on Bray-Curtis similarities of fourth root transformed data (shelf position and year, fixed factors; site random factor nested in shelf position; 9999 iterations). Herbivorous fish species consistently contributing to average similarity within assemblages across the shelf (grey boxes) in each year are listed (one-way SIMPER; sim/SD, dissim/SD > 2). Multivariate dispersion analysis (MVDISP) results shown with an index of multivariate dispersion (IMD).

	Inner	Mid	Outer
Inner	Av. sim: 2008/9: **63%**; 2016: **52%** PERMANOVA: **P=0.03** (comparison between years) IMD**:** 2008/9: **0.65**; 2016: **1.07** SIM/SD ≥2: 2008/9: ***Scarus rivulatus, Siganus doliatus, Acanthurus blochii, Scarus ghobban*** 2016: ***Scarus rivulatus***	Av. disssim: 2008/9: **66%**; 2016: **84%**	Av. disssim: 2008/9: **81%**; 2016: **97%**
Mid	IMD: 2008/9: **0.06**; 2016: **0.25** 2008/9: P: **0.0002 (MC)**; 2016: **0.002 (perm)**	Av. sim: 2008/9: **62%**; 2016: **44%** PERMANOVA: **P(MC)=0.14** (comparison between years) IMD: 2008/9: **0.71**; 2016: **1.35** SIM/SD ≥2: 2008/9: ***Zebrasoma scopas, Ctenochaetus striatus, Scarus frenatus, Acanthurus nigrofuscus, Naso unicornis, Siganus coralinus, Scarus niger, Chlorurus spilurus*** 2016: ***Acanthurus nigrofuscus***	Av. disssim: 2008/9: **62%**; 2016: **71%**
Outer	IMD: 2008/9: **-0.44** ; 2016: **-0.18** 2008/9: P: **0.0001 (MC)**; 2016: **0.0001 (MC)**	IMD: 2008/9: **0.42**; 2016: **0.49** 2008/9: P: **0.0002 (MC)**; 2016: **0.002 (perm)**	Av. sim: 2008/9: **69%**; 2016: **57%** PERMANOVA: **P=0.03** (comparison between years) IMD: 2008/9: **0.38**; 2016: **0.89** SIM/SD ≥2: 2008/9: ***Naso tonganus, Naso unicornis, Acanthurus lineatus, Chlorurus microrhinos, Ctenochaetus striatus, Acanthurus nigricans, Naso lituratus, Acanthurus triostegus*** 2016: ***Acanthurus lineatus, Ctenochaetus striatus***

Table S2.3 Pairwise comparisons (with lower and upper 95% confidence intervals: CI) of linear mixed effects models of variation in cross-shelf benthic composition and herbivorous fish assemblage structure in 2008/9 and 2016.

Response	Contrast	Contrast estimate	Lower CI	Upper CI	Test stat	*P*
Total hard coral cover (%)	Inner: 2008/9 vs 2016	-23.75	-29.8	-17.7	-7.77	<0.0001
	Mid: 2008/9 vs 2016	-42.2	-48.4	-36.01	-13.49	<0.0001
	Outer: 2008/9 vs 2016	-48.24	-54.29	-42.19	-15.79	<0.0001
Total macroalgal cover (%)	Inner: 2008/9 vs 2016	21.06	13.01	29.11	5.18	<0.0001
	Mid: 2008/9 vs 2016	-0.28	-1.4	0.85	-0.48	0.63
	Outer: 2008/9 vs 2016	-0.39	-1.06	0.28	-1.16	0.25
Shannon diversity (H)	2008/9 vs 2016	-0.43	-0.58	-0.27	-5.48	<0.0001
	Inner vs Mid	0.59	0.31	0.87	4.88	<0.0001
	Inner vs Outer	-0.19	-0.5	0.12	-1.45	0.32
	Outer vs Mid	-0.78	-1.06	-0.5	-6.46	<0.0001
Functional richness	2008/9 vs 2016	-0.16	-0.2	-0.13	-9.54	<0.0001
	Inner vs Mid	0.07	0.02	0.12	3.07	0.01
	Inner vs Outer	-0.004	-0.05	0.06	0.17	0.98
	Outer vs Mid	-0.06	-0.11	-0.01	-2.99	0.01
Functional specialisation	Inner: 2008/9 vs 2016	0.09	0.09	0.23	4.32	<0.0001
	Mid: 2008/9 vs 2016	-0.07	-0.11	-0.03	-3.35	0.001
	Outer: 2008/9 vs 2016	-0.02	-0.45	0.01	-1.54	0.13
Functional originality	Inner: 2008/9 vs 2016	-0.24	-0.37	-0.11	-3.72	0.0004
	Mid: 2008/9 vs 2016	-0.04	-0.14	0.06	-0.85	0.4
	Outer: 2008/9 vs 2016	0.01	-0.19	0.21	0.14	0.89
Total herbivores (log kg ha-1)	Inner: 2008/9 vs 2016	0.13	-0.2	0.47	0.79	0.43
	Mid: 2008/9 vs 2016	0.4	0.16	0.64	3.33	0.001
	Outer: 2008/9 vs 2016	0.84	0.51	1.17	4.98	<0.0001
Macroalgal browsers (kg ha-1)	2008/9 vs 2016	-114.28	-158.35	-70.22	-5.16	<0.0001
	Inner vs Mid	60.07	-18.71	138.85	1.74	0.17
	Inner vs Outer	1153	811.56	1494.44	7.71	<0.0001
	Outer vs Mid	1092.93	746.38	1439.48	7.2	<0.0001
Croppers (kg ha-1)	Inner: 2008/9 vs 2016	-37.65	-113.58	38.29	-0.99	0.33
	Mid: 2008/9 vs 2016	280.67	111.87	449.46	3.31	0.001
	Outer: 2008/9 vs 2016	538.67	348.9	728.433	5.65	<0.0001
Scrapers (kg ha-1)	2008/9 vs 2016	-43.94	-72.51	-15.38	-3.06	0.002
	Inner vs Mid	60.1	12.19	108.01	2.84	0.01
	Inner vs Outer	-275.64	-36.56	587.84	2	0.09
	Outer vs Mid	215.54	-99.38	530.46	1.55	0.24
Detrital feeders (kg ha-1)	Inner: 2008/9 vs 2016	0.42	-0.19	1.03	1.37	0.18
	Mid: 2008/9 vs 2016	171.76	94.92	248.6	4.45	<0.0001
	Outer: 2008/9 vs 2016	157.5	82.89	232.11	4.2	<0.0001
Excavators (kg ha-1)	2008/9 vs 2016	-8.39	-17.54	0.76	-1.82	0.07
	Inner vs Mid	87.64	38.89	136.4	4.17	<0.0001
	Inner vs Outer	108.85	61.87	155.84	5.37	<0.0001
	Outer vs Mid	21.21	-46.07	88.5	0.73	0.74

Appendix B. Supplemental information for Chapter 3:

Higher fish biomass inside than outside marine reserves despite typhoon impacts in a complex reefscape

Table S3.1. Fish species surveyed, categorized by Family

Acanthuridae
- *Acanthurus blochii*
- *Acanthurus fowleri*
- *Acanthurus lineatus*
- *Acanthurus mata*
- *Acanthurus nigricans*
- *Acanthurus nigricauda*
- *Acanthurus nigrofuscus*
- *Acanthurus olivaceus*
- *Acanthurus pyroferus*
- *Acanthurus sp.*
- *Acanthurus thompsoni*
- *Acanthurus triostegus*
- *Ctenochaetus binotatus*
- *Ctenochaetus cyanocheilus*
- *Ctenochaetus sp.*
- *Ctenochaetus striatus*
- *Ctenochaetus tominiensis*
- *Naso brevirostris*
- *Naso hexacanthus*
- *Naso lituratus*
- *Naso minor*
- *Naso sp.*
- *Naso unicornis*
- *Naso vlamingii*
- *Zebrasoma scopas*
- *Zebrasoma veliferum*

Balistidae
- *Balistoides viridescens*
- *Odonus niger*

Caesionidae
- *Caesio caerulaurea*
- *Caesio cuning*
- *Caesio lunaris*
- *Caesio sp.*
- *Caesio teres*
- *Pterocaesio lativittata*
- *Pterocaesio pisang*
- *Pterocaesio sp.*
- *Pterocaesio tessellata*
- *Pterocaesio tile*

Carangidae
- *Carangoides orthogrammus*
- *Carangoides plagiotaenia*
- *Caranx melampygus*
- *Caranx sexfasciatus*
- *Caranx sp.*
- *Elagatis bipinnulata*
- *Trachinotus blochii*

Chaetodontidae
- *Chaetodon adiergastos*
- *Chaetodon auriga*
- *Chaetodon baronessa*
- *Chaetodon bennetti*
- *Chaetodon ephippium*
- *Chaetodon kleinii*
- *Chaetodon lineolatus*
- *Chaetodon lunula*
- *Chaetodon lunulatus*
- *Chaetodon melannotus*
- *Chaetodon mertensii*
- *Chaetodon ocellicaudus*
- *Chaetodon octofasciatus*
- *Chaetodon ornatissimus*
- *Chaetodon pelewensis*
- *Chaetodon punctatofasciatus*
- *Chaetodon rafflesii*
- *Chaetodon semeion*
- *Chaetodon sp.*
- *Chaetodon speculum*
- *Chaetodon trifascialis*
- *Chaetodon ulietensis*
- *Chaetodon unimaculatus*
- *Chaetodon vagabundus*
- *Chelmon sp.*
- *Coradion sp.*
- *Forcipiger flavissimus*
- *Forcipiger longirostris*
- *Hemitaurichthys polylepis*
- *Heniochus chrysostomus*
- *Heniochus diphreutes*
- *Heniochus sp.*

Ephippidae
- *Platax sp.*

Haemulidae

Plectorhinchus chaetodonoides
Plectorhinchus lineatus
Plectorhinchus sp.
Plectorhinchus vittatus

Kyphosidae

Kyphosus cinerascens
Kyphosus sp.
Kyphosus vaigiensis

Labridae

Anampses caeruleopunctatus
Anampses geographicus
Anampses melanurus
Anampses meleagrides
Anampses meleagris
Anampses sp.
Anampses twistii
Bodianus diana
Bodianus dictynna
Bodianus mesothorax
Bodianus sp.
Cheilinus chlorourus
Cheilinus fasciatus
Cheilinus oxycephalus
Cheilinus sp.
Cheilinus trilobatus
Cheilinus undulatus
Cheilio inermis
Choerodon anchorago
Choerodon sp.
Cirrhilabrus ryukyuensis
Cirrhilabrus sp.
Coris batuensis
Coris gaimard
Diproctacanthus xanthurus
Epibulus brevis
Epibulus insidiator
Gomphosus varius
Halichoeres chrysus
Halichoeres hortulanus
Halichoeres marginatus
Halichoeres melanurus
Halichoeres nigrescens
Halichoeres podostigma

Labridae

Halichoeres prosopeion
Halichoeres richmondi
Halichoeres scapularis
Halichoeres sp.
Hemigymnus fasciatus
Hemigymnus melapterus
Hologymnosus annulatus
Hologymnosus doliatus
Hologymnosus sp.
Labrichthys unilineatus
Labrid sp.
Labroides bicolor
Labroides dimidiatus
Labroides sp.
Labropsis manabei
Labropsis xanthonota
Macropharyngodon meleagris
Macropharyngodon negrosensis
Novaculichthys taeniourus
Oxycheilinus bimaculatus
Oxycheilinus celebicus
Oxycheilinus digramma
Oxycheilinus sp.
Oxycheilinus unifasciatus
Pseudocheilinus evanidus
Pseudocheilinus hexataenia
Pseudodax moluccanus
Pseudojuloides sp.
Stethojulis bandanensis
Stethojulis interrupta
Stethojulis strigiventer
Thalassoma amblycephalum
Thalassoma hardwicke
Thalassoma jansenii
Thalassoma lunare
Thalassoma trilobatum

Labridae (Scarinae)

Calotomus carolinus
Calotomus sp.
Cetoscarus ocellatus
Chlorurus bleekeri
Chlorurus bowersi
Chlorurus microrhinos
Chlorurus sp.

Labridae (Scarinae)

Chlorurus spilurus
Cirrhilabrus sp.
Hipposcarus longiceps
Scarus chameleon
Scarus dimidiatus
Scarus flavipectoralis
Scarus forsteni
Scarus ghobban
Scarus globiceps

Mullidae

Mulloidichthys flavolineatus
Mulloidichthys sp.
Mulloidichthys vanicolensis
Parupeneus barberinoides
Parupeneus barberinus
Parupeneus crassilabris
Parupeneus cyclostomus
Parupeneus multifasciatus

Scarus hypselopterus
Scarus niger
Scarus oviceps
Scarus prasiognathos
Scarus psitticus
Scarus rivulatus
Scarus schlegeli
Scarus sp.
Scarus spinus
Scarus tricolor

Lethrinidae
Lethrinus erythracanthus
Lethrinus erythropterus
Lethrinus harak
Lethrinus obsoletus
Lethrinus ornatus
Lethrinus sp.
Monotaxis grandoculis
Monotaxis heterodon

Lutjanidae
Aprion virescens
Lutjanus argentimaculatus
Lutjanus biguttatus
Lutjanus bohar
Lutjanus decussatus
Lutjanus ehrenbergii
Lutjanus fulviflamma
Lutjanus fulvus
Lutjanus gibbus
Lutjanus guttatus
Lutjanus kasmira
Lutjanus monostigma
Lutjanus sp.
Macolor macularis

Parupeneus sp.

Nemipteridae
Scolopsis bilineatus
Scolopsis sp.

Plotosidae
Plotosus lineatus

Pomacanthidae
Apolemichthys trimaculatus
Centropyge bicolor
Centropyge bispinosa
Centropyge nox
Centropyge sp.
Centropyge tibicen
Centropyge vrolikii
Chaetodontoplus mesoleucus
Genicanthus lamarck
Pomacanthus imperator
Pomacanthus navarchus
Pomacanthus semicirculatus
Pomacanthus sexstriatus
Pomacanthus xanthometopon
Pygoplites diacanthus

Pomacentridae
Amblyglyphidodon aureus
Amblyglyphidodon curacao
Amblyglyphidodon leucogaster
Amphiprion ocellaris
Amphiprion sp.
Chromis amboinensis
Chromis analis
Chromis atripectoralis
Chromis lepidolepis

Pomacentridae
Chromis margaritifer
Chromis reticulatus
Chromis retrofasciata
Chromis sp.
Chromis ternatensis
Chromis viridis
Chromis weberi
Chromis xanthura
Chrysiptera rollandi
Chrysiptera springeri
Chrysiptera talboti
Dascyllus aruanus
Dascyllus reticulatus
Dascyllus trimaculatus
Dischistodus melanotus
Dischistodus perspicillatus
Hemiglyphidodon plagiometopon
Neoglyphidodon melas
Neoglyphidodon nigroris
Neopomacentrus sp.
Plectroglyphidodon lacrymatus

Serranidae
Cephalopholis sexmaculata
Cephalopholis urodeta
Epinephelus erythrurus
Epinephelus fasciatus
Epinephelus merra
Epinephelus ongus
Epinephelus polyphekadion
Epinephelus sp.
Gracila albomarginata
Plectropomus areolatus
Plectropomus laevis
Plectropomus leopardus
Plectropomus oligacanthus
Plectropomus sp.
Variola louti

Serranidae (Anthiinae)
Pseudanthias huchtii
Pseudanthias pascalus
Pseudanthias sp.
Pseudanthias squamipinnis

Plectroglyphidodon sp.
Pomacentrus adelus
Pomacentrus alexanderae
Pomacentrus amboinensis
Pomacentrus bankanensis
Pomacentrus brachialis
Pomacentrus coelestis
Pomacentrus lepidogenys
Pomacentrus moluccensis
Pomacentrus nagasakiensis
Pomacentrus sp.
Pomacentrus stigma
Stegastes sp.

Scombridae
Rastrelliger kanagurta
Rastrelliger sp.

Serranidae
Aethaloperca rogaa
Cephalopholis argus
Cephalopholis cyanostigma
Cephalopholis microprion
Cephalopholis miniata
Pseudanthias tuka

Siganidae
Siganus corallinus
Siganus doliatus
Siganus guttatus
Siganus puellus
Siganus punctatissimus
Siganus punctatus
Siganus sp.
Siganus spinus
Siganus unimaculatus
Siganus vermiculatus
Siganus virgatus
Siganus vulpinus

Sphyraenidae
Sphyraena obtusata
Sphyraena sp.

Zanclidae
Zanclus cornutus

Table S3.2. Pairwise comparisons of PERMANOVA with Monte Carlo sampling, for response variables of benthic cover, all fish density, and large fish biomass.

Response	Zone	Pairwise comparison	df	*t*	perms	*P*(MC)	*Sig.*
Benthic % Cover	Crest	No Typhoon vs Typhoon	112	5.2714	9956	0.001	*
	Slope	No Typhoon vs Typhoon	112	4.8063	9945	0.001	*
	Crest	No Typhoon: Mainland vs Offshore	75	3.2251	9953	0.001	*
		Typhoon: Mainland vs Offshore	35	1.1891	9953	0.213	
	Slope	No Typhoon: Mainland vs Offshore	75	1.8189	9951	0.009	*
		Typhoon: Mainland vs Offshore	35	2.0477	9952	0.002	*
	Crest	No Typhoon, Mainland: NTMR vs Fished	52	1.1887	9957	0.219	
		Typhoon, Mainland: NTMR vs Fished	28	1.3996	9958	0.114	
		No Typhoon, Offshore: NTMR vs Fished	21	2.3212	9917	0.001	*
		Typhoon, Offshore: NTMR vs Fished	5	3.7713	35	0.003	*
	Slope	No Typhoon, Mainland: NTMR vs Fished	52	1.5936	9954	0.036	*
		Typhoon, Mainland: NTMR vs Fished	28	1.2439	9956	0.183	
		No Typhoon, Offshore: NTMR vs Fished	21	1.2405	9909	0.195	
		Typhoon, Offshore: NTMR vs Fished	5	4.9751	35	0.001	*
All Fish Species, Density	Crest	No Typhoon vs Typhoon	109	3.12	9906	0.001	*
	Slope	No Typhoon vs Typhoon	109	2.6628	9921	0.001	*
	Crest	No Typhoon: Mainland vs Offshore	72	2.0754	9882	0.001	*
		Typhoon: Mainland vs Offshore	35	1.6893	9895	0.002	*
	Slope	No Typhoon: Mainland vs Offshore	72	3.0486	9901	0.001	*
		Typhoon: Mainland vs Offshore	35	1.9064	9917	0.002	*
	Crest	No Typhoon, Mainland: NTMR vs Fished	49	1.0752	9894	0.284	
		Typhoon, Mainland: NTMR vs Fished	28	1.298	9904	0.080	
		No Typhoon, Offshore: NTMR vs Fished	21	1.5181	9871	0.015	*
		Typhoon, Offshore: NTMR vs Fished	5	1.5942	35	0.069	
	Slope	No Typhoon, Mainland: NTMR vs Fished	49	1.1767	9902	0.126	
		Typhoon, Mainland: NTMR vs Fished	28	1.2352	9919	0.130	
		No Typhoon, Offshore: NTMR vs Fished	21	1.488	9894	0.038	*
		Typhoon, Offshore: NTMR vs Fished	5	1.3819	35	0.142	
Large Fish Species, Biomass	Crest	No Typhoon vs Typhoon	112	2.5607	9989	0.001	*
	Slope	No Typhoon vs Typhoon	112	2.1541	9890	0.001	*
	Crest	No Typhoon: Mainland vs Offshore	75	1.9215	9885	0.001	*
		Typhoon: Mainland vs Offshore	35	1.8738	9903	0.001	*
	Slope	No Typhoon: Mainland vs Offshore	75	2.5948	9905	0.001	*
		Typhoon: Mainland vs Offshore	35	1.9356	9887	0.001	*
	Crest	No Typhoon, Mainland: NTMR vs Fished	52	1.1282	9905	0.193	
		Typhoon, Mainland: NTMR vs Fished	28	1.592	9912	0.006	*
		No Typhoon, Offshore: NTMR vs Fished	21	1.5634	9840	0.005	*
		Typhoon, Offshore: NTMR vs Fished	5	1.3658	35	0.146	
	Slope	No Typhoon, Mainland: NTMR vs Fished	52	1.1434	9888	0.154	
		Typhoon, Mainland: NTMR vs Fished	28	1.3604	9926	0.048	*
		No Typhoon, Offshore: NTMR vs Fished	21	1.7025	9869	0.006	*
		Typhoon, Offshore: NTMR vs Fished	5	1.4446	35	0.105	

Appendix S3.3. Planned comparisons of percent benthic cover for each predictor variable in generalized linear mixed effects models.

Response	Reef Zone	Planned comparison	Contrast estimate[1]	Lower 95% CI	Upper 95% CI	Sig.
Fragile Hard Corals *(Branching-Tabulate-Foliose)*	Crest	Mainland: No Typhoon vs Typhoon	3.54	1.44	8.70	*
		Offshore: No Typhoon vs Typhoon	20.53	9.03	46.68	*
	Slope	Mainland: No Typhoon vs Typhoon	2.47	1.30	4.70	*
		Offshore: No Typhoon vs Typhoon	6.93	3.27	14.67	*
	Crest	No Typhoon: Mainland vs Offshore	2.51	0.98	6.47	
		Yes Typhoon: Mainland vs Offshore	0.43	0.12	1.51	
	Slope	No Typhoon: Mainland vs Offshore	1.67	0.84	3.29	
		Yes Typhoon: Mainland vs Offshore	0.59	0.22	1.57	
Robust Hard Corals *(Massive-Encrusting)*	Crest	Mainland: No Typhoon vs Typhoon	3.12	1.82	5.34	*
		Offshore: No Typhoon vs Typhoon	2.52	1.31	4.83	*
	Slope	Mainland: No Typhoon vs Typhoon	3.12	1.94	5.01	*
		Offshore: No Typhoon vs Typhoon	2.45	1.57	3.83	*
	Crest	No Typhoon: Mainland vs Offshore	1.71	0.96	3.04	
		Yes Typhoon: Mainland vs Offshore	1.38	0.61	3.13	
	Slope	No Typhoon: Mainland vs Offshore	0.91	0.43	1.93	
		Yes Typhoon: Mainland vs Offshore	0.62	0.30	1.31	
Macroalgae	Crest	Mainland: Fished vs NTMR	1.71	1.17	2.50	*
		Offshore: Fished vs NTMR	1.42	0.72	2.79	
	Slope	Mainland: Fished vs NTMR	1.74	1.13	2.66	*
		Offshore: Fished vs NTMR	1.21	0.56	2.63	
	Crest	Fished: Mainland vs Offshore	2.03	0.79	5.20	
		NTMR: Mainland vs Offshore	1.68	0.65	4.36	
	Slope	Fished: Mainland vs Offshore	5.22	1.50	18.15	*
		NTMR: Mainland vs Offshore	3.64	1.03	12.80	*

[1]*Contrast estimates represent the number of times one level of the response was higher than the other rather than the absolute difference, with lower and upper 95% confidence intervals (CI).*

Appendix C. Supplemental information for Chapter 4: Environmental factors have a greater influence on reef fish density and richness than fishing

Table S4.1 Fish species in each trophic group

Trophic group	Family	Genus species
Targeted Mesopredators	Carangidae	*Carangoides plagiotaenia*
		Caranx melampygus
		Caranx sexfasciatus
		Caranx sp.
		Elagatis bipinnulata
	Lethrinidae	*Lethrinus erythracanthus*
		Lethrinus erythropterus
		Lethrinus harak
		Lethrinus obsoletus
		Lethrinus ornatus
		Lethrinus sp.
	Lutjanidae	*Aprion virescens*
		Lutjanus argentimaculatus
		Lutjanus biguttatus
		Lutjanus bohar
		Lutjanus decussatus
		Lutjanus ehrenbergii
		Lutjanus fulviflamma
		Lutjanus fulvus
		Lutjanus gibbus
		Lutjanus kasmira
		Lutjanus monostigma
		Lutjanus sp.
		Macolor macularis
	Serranidae	*Aethaloperca rogaa*
		Cephalopholis argus
		Cephalopholis cyanostigma
		Cephalopholis microprion
		Cephalopholis miniata
		Cephalopholis sexmaculata
		Cephalopholis urodeta
		Epinephelus erythrurus
		Epinephelus fasciatus
		Epinephelus merra
		Epinephelus polyphekadion
		Epinephelus sp.
		Gracila albomarginata
		Plectropomus areolatus
		Plectropomus laevis
		Plectropomus leopardus
		Plectropomus oligacanthus
		Plectropomus sp.
		Variola louti
	Sphyraenidae	*Sphyraena obtusata*
		Sphyraena sp.

Trophic group	Family	Genus species
Targeted Grazer/ detritivore	Acanthuridae	*Acanthurus blochii*
		Acanthurus fowleri
		Acanthurus lineatus
		Acanthurus nigricans
		Acanthurus nigricauda
		Acanthurus nigrofuscus
		Acanthurus olivaceus
		Acanthurus pyroferus
		Acanthurus triostegus
		Ctenochaetus binotatus
		Ctenochaetus sp.
		Ctenochaetus striatus
		Ctenochaetus tominiensis
		Zebrasoma scopas
		Zebrasoma veliferum
	Pomacanthidae	*Centropyge bicolor*
		Centropyge bispinosa
		Centropyge nox
		Centropyge sp.
		Centropyge tibicen
		Centropyge vrolikii
	Pomacentridae	*Hemiglyphidodon plagiometopon*
	Siganidae	*Siganus corallinus*
		Siganus doliatus
		Siganus guttatus
		Siganus puellus
		Siganus punctatissimus
		Siganus punctatus
		Siganus sp.
		Siganus spinus
		Siganus unimaculatus
		Siganus vermiculatus
		Siganus virgatus
		Siganus vulpinus

Trophic group	Family	Genus species
Targeted Large-bodied planktivores	Acanthuridae	*Acanthurus mata*
		Acanthurus thompsoni
		Naso brevirostris
		Naso hexacanthus
		Naso minor
		Naso vlamingii
	Balistidae	*Odonus niger*
	Caesionidae	*Caesio caerulaurea*
		Caesio cuning
		Caesio lunaris
		Caesio sp.
		Caesio teres
		Pterocaesio lativittata
		Pterocaesio pisang
		Pterocaesio sp.
		Pterocaesio tessellata
		Pterocaesio tile
	Chaetodontidae	*Hemitaurichthys polylepis*
		Heniochus diphreutes
	Pomacanthidae	*Genicanthus lamarck*
	Scombridae	*Rastrelliger kanagurta*
		Rastrelliger sp.

Trophic group	Family	Genus species
Targeted Scrapers	Labridae (Scarinae)	*Hipposcarus longiceps*
		Scarus chameleon
		Scarus dimidiatus
		Scarus flavipectoralis

		Scarus forsteni
		Scarus ghobban
		Scarus globiceps
		Scarus hypselopterus
		Scarus niger
		Scarus oviceps
		Scarus prasiognathos
		Scarus psitticus
		Scarus rivulatus
		Scarus schlegeli
		Scarus sp.
		Scarus spinus
		Scarus tricolor

Trophic group	Family	Genus species
Non-targeted invertivores	Balistidae	*Balistoides viridescens*
	Chaetodontidae	*Forcipiger flavissimus*
		Forcipiger longirostris
	Labridae	*Anampses caeruleopunctatus*
		Anampses geographicus
		Anampses melanurus
		Anampses meleagrides
		Anampses sp.
		Anampses twistii
		Bodianus diana
		Bodianus dictynna
		Bodianus mesothorax
		Bodianus sp.
		Cheilio inermis
		Choerodon anchorago
		Choerodon sp.
		Coris batuensis
		Coris gaimard
		Epibulus brevis
		Gomphosus varius
		Halichoeres chrysus
		Halichoeres hortulanus
		Halichoeres marginatus
		Halichoeres melanurus
		Halichoeres nigrescens
		Halichoeres podostigma
		Halichoeres prosopeion
		Halichoeres richmondi
		Halichoeres scapularis
		Halichoeres sp.
		Hemigymnus fasciatus
		Hemigymnus melapterus
		Macropharyngodon meleagris
		Macropharyngodon negrosensis
		Stethojulis bandanensis
		Stethojulis interrupta
		Stethojulis strigiventer
		Thalassoma amblycephalum
		Thalassoma hardwicke
		Thalassoma jansenii
		Thalassoma lunare
		Thalassoma trilobatum

Non-targeted fish ≤10cm TL	Family	Genus species
	Acanthuridae	*Acanthurus nigricans*
		Acanthurus nigrofuscus
		Acanthurus pyroferus
		Acanthurus sp.
		Acanthurus thompsoni
		Ctenochaetus binotatus
		Ctenochaetus cyanocheilus
		Ctenochaetus sp.
		Ctenochaetus striatus
		Ctenochaetus tominiensis
		Naso lituratus
		Naso sp.
		Zebrasoma scopas
	Chaetodontidae	*Chaetodon baronessa*
		Chaetodon kleinii
		Chaetodon lunulatus
		Chaetodon melannotus
		Chaetodon mertensii
		Chaetodon octofasciatus
		Chaetodon ornatissimus
		Chaetodon pelewensis
		Chaetodon punctatofasciatus
		Chaetodon sp.
		Chaetodon vagabundus
		Hemitaurichthys polylepis
		Heniochus chrysostomus
		Heniochus sp.
	Ephippidae	*Platax sp.*
	Haemulidae	*Plectorhinchus chaetodonoides*
		Plectorhinchus sp.
	Labridae	*Anampses geographicus*
		Anampses melanurus
		Anampses meleagrides
		Anampses sp.
		Anampses twistii
		Bodianus dictynna
		Bodianus mesothorax
		Bodianus sp.
		Cheilinus fasciatus
		Cheilinus oxycephalus
		Cheilinus trilobatus
		Cirrhilabrus ryukyuensis
		Cirrhilabrus sp.
		Coris batuensis
		Coris gaimard
		Diproctacanthus xanthurus
		Epibulus brevis
		Gomphosus varius
		Halichoeres chrysus
		Halichoeres hortulanus
		Halichoeres melanurus
		Halichoeres podostigma
		Halichoeres prosopeion
		Halichoeres richmondi
		Halichoeres scapularis
		Halichoeres sp.
		Hemigymnus fasciatus
		Hemigymnus melapterus
		Hologymnosus doliatus
		Hologymnosus sp.
		Labrichthys unilineatus
		Labrid sp.
		Labroides dimidiatus
		Labroides sp.
		Labropsis xanthonota
		Macropharyngodon meleagris
		Macropharyngodon negrosensis
		Oxycheilinus bimaculatus
		Oxycheilinus digramma
		Oxycheilinus sp.
		Oxycheilinus unifasciatus
		Pseudocheilinus evanidus
		Pseudocheilinus hexataenia
		Pseudojuloides sp.
		Stethojulis bandanensis
		Stethojulis interrupta
		Stethojulis strigiventer
		Thalassoma amblycephalum
		Thalassoma hardwicke
		Thalassoma jansenii

	Thalassoma lunare			*Chromis sp.*
Labridae				*Chromis ternatensis*
(Scarinae)	*Cetoscarus ocellatus*			*Chromis viridis*
	Chlorurus bleekeri			*Chromis weberi*
	Chlorurus bowersi			*Chromis xanthura*
	Chlorurus microrhinos			*Chrysiptera rollandi*
	Chlorurus sp.			*Chrysiptera springeri*
	Chlorurus spilurus			*Chrysiptera talboti*
	Cirrhilabrus sp.			*Dascyllus aruanus*
	Scarus dimidiatus			*Dascyllus reticulatus*
	Scarus flavipectoralis			*Dascyllus trimaculatus*
	Scarus forsteni			*Neoglyphidodon melas*
	Scarus ghobban			*Neoglyphidodon nigroris*
	Scarus hypselopterus			*Neopomacentrus sp.*
	Scarus niger			*Plectroglyphidodon lacrymatus*
	Scarus psitticus			*Plectroglyphidodon sp.*
	Scarus rivulatus			*Pomacentrus adelus*
	Scarus sp.			*Pomacentrus alexanderae*
	Scarus tricolor			*Pomacentrus amboinensis*
Lethrinidae	*Lethrinus erythracanthus*			*Pomacentrus bankanensis*
	Lethrinus harak			*Pomacentrus brachialis*
Lutjanidae	*Lutjanus bohar*			*Pomacentrus coelestis*
	Macolor macularis			*Pomacentrus lepidogenys*
Mullidae	*Parupeneus barberinus*			*Pomacentrus moluccensis*
	Parupeneus multifasciatus			*Pomacentrus nagasakiensis*
Nemipteridae	*Scolopsis bilineatus*			*Pomacentrus sp.*
Pomacanthidae	*Centropyge bicolor*			*Pomacentrus stigma*
	Centropyge bispinosa			*Stegastes sp.*
	Centropyge nox		Serranidae	*Cephalopholis argus*
	Centropyge tibicen			*Cephalopholis microprion*
	Centropyge vrolikii			*Cephalopholis urodeta*
	Chaetodontoplus mesoleucus			*Epinephelus merra*
	Genicanthus lamarck			*Epinephelus sp.*
	Pygoplites diacanthus			*Plectropomus leopardus*
Pomacentridae	*Amblyglyphidodon aureus*			*Variola louti*
	Amblyglyphidodon curacao		Serranidae	
	Amblyglyphidodon leucogaster		(Anthiinae)	*Pseudanthias huchtii*
	Amphiprion ocellaris			*Pseudanthias pascalus*
	Amphiprion sp.			*Pseudanthias sp.*
	Chromis amboinensis			*Pseudanthias squamipinnis*
	Chromis atripectoralis			*Pseudanthias tuka*
	Chromis lepidolepis		Siganidae	*Siganus sp.*
	Chromis margaritifer			*Siganus unimaculatus*
	Chromis reticulatus			*Siganus vulpinus*
	Chromis retrofasciata		Zanclidae	*Zanclus cornutus*

Appendix D: Supplemental information for Chapter 5

Using environmental indicators to investigate dietary plasticity in important coral reef fisheries species inhabiting different environmental conditions

Table S5.1 Details of fish species collected from each low (L) and high (H) input site 1. Bonbonon, 2. Apo, 3. Tubod, 4. Paliton, 5. Cangbagsa

Species/ Diet group	Site	*n*	FL range(mm)	Nitrogen (δ15N)		Carbon (δ13C)		Age (years)	
				Mean	Range	Mean	Range	Mean	Range
Naso unicornis/	1(H)	4	124-252	7.60	7.0: 8.4	-9.90	-8.9: -10.9	3.0	1-5
Browser	2(L)	6	248-343	7.10	6.3: 7.8	-11.60	-10.5: -12.1	7.4	2-12
	3(H)	5	163-355	7.30	6.9: 7.6	-9.70	-9.3: -10.0	2.0	1-5
	4(L)	9	135-192	6.50	6.1: 6.9	-10.40	-9.6: -11.2	1.5	1-4
	5(H)	3	169-198	6.70	6.5: 7.1	-10.00	-9.1: -10.9	1.0	1-1
Siganus virgatus/	1(H)	12	121-212	7.30	6.2: 8.1	-13.45	-11.9: -14.6	3.5	1-7
Cropper	2(L)	7	168-208	6.90	6.5: 7.5	-14.60	-13.8: -15.2	5.5	5-6
	3(H)	11	143-168	6.90	5.6: 8.8	-14.80	-13.0: -15.7	2.7	1-4
	4(L)	26	134-180	6.50	5.4: 7.7	-14.63	-13.2: -15.9	2.3	1-5
	5(H)	25	133-207	6.91	6.2: 8.2	-14.00	-12.5: -15.6	3.2	2-6
Naso minor/	1(H)	13	180-217	9.60	9.1: 9.9	-17.50	-17.1: -17.7	4.5	2-7
Planktivore	2(L)	19	161-196	9.70	9.0: 10.2	-17.50	-17.2: -17.9	4.0	1-8
	3-4(H-L)	9	170-217	9.70	9.2: 10.0	-17.40	-17.1: -17.6	4.1	1-11

Table S5.2 Tukey pairwise comparison of sedimentation rates, and Sargassum $\delta^{15}N$ among sites

Response	Site1	Site2	Estimate	Std. Error	z value	Pr(>|z|)	Sig.
Sediment	Bonbonon	Apo	0.000	0.003	-0.170	1.000	
	Cangbagsa	Apo	0.009	0.002	3.977	<0.001	***
	Paliton	Apo	-0.002	0.002	-0.679	0.984	
	Tubod	Apo	0.021	0.002	9.491	<0.001	***
	Tulapos	Apo	-0.002	0.002	-0.775	0.972	
	Cangbagsa	Bonbonon	0.009	0.003	3.727	0.003	**
	Paliton	Bonbonon	-0.001	0.003	-0.437	0.998	
	Tubod	Bonbonon	0.022	0.003	8.658	<0.001	***
	Tulapos	Bonbonon	-0.001	0.003	-0.524	0.995	
	Paliton	Cangbagsa	-0.011	0.002	-4.656	<0.001	***
	Tubod	Cangbagsa	0.012	0.002	5.514	<0.001	***
	Tulapos	Cangbagsa	-0.011	0.002	-4.753	<0.001	***
	Tubod	Paliton	0.023	0.002	10.170	<0.001	***
	Tulapos	Paliton	0.000	0.002	-0.097	1.000	
	Tulapos	Tubod	-0.023	0.002	-10.266	<0.001	***
Sargassum $\delta^{15}N$	Bonbonon	Cangbagsa	-0.43	0.13	-3.25	0.01	*
	Paliton	Cangbagsa	-1.27	0.13	-9.50	<0.001	***
	Tubod	Cangbagsa	0.13	0.13	1.00	0.86	
	Tulapos	Cangbagsa	-1.27	0.13	-9.50	<0.001	***
	Paliton	Bonbonon	-0.83	0.13	-6.25	<0.001	***
	Tubod	Bonbonon	0.57	0.13	4.25	<0.001	***
	Tulapos	Bonbonon	-0.83	0.13	-6.25	<0.001	***
	Tubod	Paliton	1.40	0.13	10.50	<0.001	***
	Tulapos	Paliton	0.00	0.13	0.00	1.00	
	Tulapos	Tubod	-1.40	0.13	-10.50	<0.001	***

Table S5.3 Planned comparisons of: turf algal Biomass (g/m^2) between Sites for caged treatments, Yield to Grazers at each site, Production at each site

Response	Comparison		estimate	lower 95% conf.int	upper 95% conf.int	Sig.
Biomass	Caged Tile Treatments	Apo-Bonbonon	15.47	0.79	31.74	*
		Apo-Cangbagsa	8.71	-7.56	24.97	
		Apo-Paliton	-33.10	-49.37	-16.84	*
		Apo-Tubod	-22.98	-40.23	-5.73	*
		Apo-Tulapos	-21.21	-37.92	-4.49	*
		Cangbagsa-Bonbonon	6.77	-9.50	23.03	
		Tubod-Bonbonon	38.46	21.20	55.71	*
		Paliton-Bonbonon	48.58	32.31	64.84	*
		Tulapos-Bonbonon	36.68	19.97	53.39	*
		Tubod-Cangbagsa	31.69	14.44	48.94	*
		Paliton-Cangbagsa	41.81	25.54	58.07	*
		Tulapos-Cangbagsa	29.91	13.20	46.62	*
		Tulapos-Paliton	-11.90	-28.61	4.81	
		Tubod-Paliton	-10.12	-27.37	7.13	
		Tubod-Tulapos	1.78	-15.90	19.45	
Yield to Grazers	Apo	Caged-Uncaged	22.66	6.77	38.55	*
	Bonbonon	Caged-Uncaged	7.27	-8.62	23.16	
	Cangbagsa	Caged-Uncaged	14.95	-1.31	31.21	
	Paliton	Caged-Uncaged	47.91	31.20	64.63	*
	Tubod	Caged-Uncaged	36.47	18.79	54.14	*
	Tulapos	Caged-Uncaged	29.47	12.76	46.18	*
Production	Apo	Caged-Standing Crop	26.45	9.74	43.16	*
	Bonbonon	Caged-Standing Crop	7.38	-9.87	24.63	
	Cangbagsa	Caged-Standing Crop	0.70	-17.23	18.62	
	Paliton	Caged-Standing Crop	56.31	39.06	73.56	*
	Tubod	Caged-Standing Crop	47.43	29.76	65.10	*
	Tulapos	Caged-Standing Crop	26.10	8.96	43.24	*

Table S5.4 siar model outputs

Fish Consumer	Site	Source	Low 95%	High 95%	mode	mean
Naso unicornis	Bonbonon	PlanktonG1	0.00	0.38	0.04	0.18
		SargassumG1	0.00	0.47	0.28	0.24
		TurfG1	0.03	0.57	0.31	0.32
		DetritusG1	0.00	0.51	0.29	0.26
	Apo	PlanktonG2	0.00	0.22	0.03	0.09
		SargassumG2	0.01	0.48	0.31	0.26
		TurfG2	0.25	0.60	0.41	0.42
		DetritusG2	0.00	0.44	0.23	0.23
	Tubod	PlanktonG3	0.00	0.27	0.03	0.11
		SargassumG3	0.00	0.43	0.27	0.22
		TurfG3	0.18	0.63	0.37	0.40
		DetritusG3	0.01	0.49	0.28	0.27
	Paliton	PlanktonG4	0.00	0.14	0.01	0.05
		SargassumG4	0.00	0.37	0.20	0.19
		TurfG4	0.40	0.72	0.57	0.56
		DetritusG4	0.00	0.40	0.13	0.20
	Cangbagsa	PlanktonG5	0.00	0.27	0.02	0.10
		SargassumG5	0.00	0.42	0.10	0.20
		TurfG5	0.18	0.74	0.44	0.45
		DetritusG5	0.00	0.49	0.30	0.25
Siganus virgatus	Bonbonon	PlanktonG1	0.01	0.29	0.15	0.16
		SargassumG1	0.10	0.67	0.36	0.38
		TurfG1	0.17	0.45	0.31	0.31
		DetritusG1	0.00	0.33	0.11	0.16
	Apo	PlanktonG2	0.04	0.40	0.25	0.23
		SargassumG2	0.00	0.51	0.29	0.27
		TurfG2	0.11	0.50	0.30	0.31
		DetritusG2	0.00	0.39	0.20	0.19
	Tubod	PlanktonG3	0.13	0.45	0.31	0.29
		SargassumG3	0.02	0.61	0.30	0.32
		TurfG3	0.06	0.40	0.24	0.23
		DetritusG3	0.00	0.32	0.15	0.16
	Paliton	PlanktonG4	0.10	0.36	0.25	0.23
		SargassumG4	0.17	0.71	0.41	0.43
		TurfG4	0.09	0.37	0.24	0.23
		DetritusG4	0.00	0.22	0.07	0.10
	Cangbagsa	PlanktonG5	0.09	0.35	0.21	0.22
		SargassumG5	0.02	0.54	0.31	0.29
		TurfG5	0.22	0.52	0.34	0.36
		DetritusG5	0.00	0.28	0.06	0.13
Naso minor	Bonbonon	PlanktonG1	0.48	0.78	0.62	0.63
		SargassumG1	0.05	0.47	0.31	0.27
		TurfG1	0.00	0.09	0.01	0.03
		DetritusG1	0.00	0.17	0.02	0.07
	Apo	PlanktonG2	0.49	0.77	0.61	0.62
		SargassumG2	0.08	0.47	0.31	0.29
		TurfG2	0.00	0.08	0.01	0.03
		DetritusG2	0.00	0.16	0.02	0.06
	Tubod-Paliton	PlanktonG3	0.42	0.79	0.60	0.60
		SargassumG3	0.01	0.48	0.29	0.26
		TurfG3	0.00	0.12	0.01	0.05
		DetritusG3	0.00	0.21	0.02	0.09